A CONCEPTUAL MODEL OF SPRINGS ECOSYSTEM ECOLOGY: TASK 1B FINAL REPORT

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Prepared by:

Lawrence E. Stevens and Abraham E. Springer
Northern Arizona University
Flagstaff, AZ 86011
(928) 523-9011
abe.spring@nau.edu
farvana@commspeed.net

Prepared for:

The National Park Service
Attn: Ms. Angela Evenden and Ms. Lisa Thomas
Cooperative Ecosystem Studies Unit
Northern Arizona University
Flagstaff, AZ 86011
(928) 556-9011
lisa_thomas@nps.gov
angela_evenden@nps.gov

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Introduction

Springs ecosystems are ecosystems in which groundwater reaches the earth's surface, often through complex and sometimes lengthy flow paths through subsurface structural, geochemical and geomorphic environments (Kreamer and Springer, in prep.; Springer et al. in prep.). At their orifices (points of emergence), the physical geomorphic template allows some springs to support numerous habitats and large arrays of aquatic, wetland and terrestrial species. Many springs serve as paleorefugia (*sensu* Nekola 1999) and as long-term stable habitats in which the evolutionary processes of natural selection, isolation, and adaptation (sometimes to extreme environmental conditions) are coupled to assemblage composition through island biogeographic and historical community development processes. In ecological time and space, springs in arid regions may serve as keystone ecosystems (*sensu* Perla and Stevens 2002), sometimes providing the only available water and habitat in the landscape for many plant and animal species. In relation to the surrounding upland ecosystems; the steep slopes of moisture, soil, biodiversity, competition, and productivity gradients at springs create severe ecotonal boundaries. Many springs emerge in freshwater or marine settings, and recent information on subaqueous springs demonstrates many parallels with those of subaerial springs, including high levels of biodiversity, species packing, productivity and endemism.

Odum's (1957) studies of Silver Springs in Florida laid the foundation for much of the science of ecosystem ecology, but springs ecosystem ecology has received relatively little attention since that time. Several symposia and survey studies of springs were conducted in the United States (Williams and Danks 1991, Van Der Kamp 1995, Botosaneanu 1998), but springs ecosystem ecology in general remains unsynthesized and relatively poorly studied. For example, recent texts on the freshwater ecoregions and legal protection of wetlands scarcely mentions springs ecosystems (e.g., Shine and de Klemm 1999; Abel et al. 2000). The scope of most previous work has been on a relatively small suite of physical characteristics of springs (e.g., flow and water quality, Meinzer 1923, Mundorff 1971), individual taxa or biota (e.g., Trichoptera, Erman 1992, 1998; aquatic snails, Hershler 1994, Hershler et al. 1999, Hershler and Sada 2002; aquatic invertebrates, Williams and Danks 1991, Ferrington 1995), or on selected topics at local or, at best, regional scales (e.g., Odum 1957, Welsh 1989; Erman 1998, Hershler et al. 2002). Virtually all studies conducted in recent decades have recognized the threatened ecological condition of springs ecosystems and the imperiled state of their biota (e.g., Minckley and Unmack 2000). However, human demands for water often preclude ecological protection of springs, and the complex, highly multi-disciplinary nature of springs ecosystem research has retarded development of a comprehensive, conceptual approach to understanding springs as ecosystems.

Here we present a general conceptual model of terrestrial springs ecosystems, with emphasis on the array of springs types that occur on the Colorado Plateau. We developed a general model from a suite of static, probabilistic, and dynamic models to relate natural ecosystem processes and components to a state-and-transition framework of human impacts on springs ecosystems. Although this modeling effort is unlikely to provide detailed predictive capability in the near future, it is likely to expose gaps in knowledge, uncertainty, and previously unrecognized interrelationships among springs ecosystems processes and components. This is a first effort, and one that will be substantially improved as additional data become available.

Ecosystem conceptual models

Purposes of Conceptual Modeling

Ecosystem models are commonly used to examine the magnitude and duration of management effects on ecosystem processes, and such models can help focus monitoring and research agendas (Walters et al. 2000, Gross 2003). As a result, conceptual modeling has been recommended to clarify stream-riparian and springs information needs and management strategies on the Colorado Plateau. Proponents of scientific ecosystem management have long emphasized the importance of such modeling exercises (Holling 1978; Walters 1986). Because ecosystem processes are often poorly understood, the purpose of ecosystem modeling generally is not to make precise quantitative predictions about specific management actions. Rather, it is to expose gaps in data and understanding, and to help evaluate general policy options (Walters et al. 2000). Presumably, as conceptual models are refined, predictive modeling may become possible. Given the present limited understanding of springs ecosystem ecology, the development of a draft conceptual springs ecosystem model will serve to stimulate discussion among springs ecosystem stakeholders and managers.

Types of Conceptual Ecosystem Models

Many different kinds of ecosystem models have been developed, from crude verbal models that outline dominant processes, to highly sophisticated multi-scale numeric models that quantitatively describe and predict management impacts on the properties and processes of complex ecosystems (Miller and Thomas 2003, De Young et al. 2004). Gross (2003) emphasizes the combined use of controls and stressor models in the initial formulation of conceptual models. His control models involve a suite of linked static / descriptive, probabilistic, or dynamics submodels that govern natural ecosystem functions and characteristics. Static ecosystem submodels describe relatively unchanging physical features or relationships of the environment, such as the distribution and permeability of geologic strata, the density of springs in a region, or landscape configuration (e.g., springs on cliff-faces, channel floors, or valley bottoms). Probabilistic submodels are those based on the chance of occurrence of physical phenomena, such as flood recurrence, rockfall, or fire frequency. Dynamic submodels relate the responses of key ecosystem components or processes to other individual or interacting components and/or processes. Each type of control model type has driving variables, some of which create driver interactions variables, as well as outputs, and ecosystem consequences.

Stressor models, particularly of anthropogenic impacts, are overlaid on the controls model, and are useful for predicting ecosystem changes in response to environmental alterations. The resulting conceptual model is likely to be most useful for identifying the inventory, assessment, monitoring, and research priorities for ecosystem managers. With sufficient baseline data, this conceptual springs ecosystem model eventually also may be able to provide quantitative predictions on ecosystem responses to environmental changes.

Conceptual Model Outputs

Springs ecosystem modeling outputs should be focused on clearly defined scientific and management hypotheses, including tests of theory as well as anthropogenic impacts on resources of concern, particularly ecosystem goods and services that can be monitored. Therefore, model outputs may include some or all of the following variables: 1) flow relationships (groundwater table elevation, aquifer responsiveness, discharge volume and variability; 2) water quality (i.e., temperature, geochemistry, bacteriology, and pollutant concentrations); 3) microhabitat area (cave, orifice, backwall, open water – lentic and lotic, wetlands, riparian) and quality (e.g., soil quality, nutrient availability); 4) keystone ecosystem linkages to the surrounding uplands, such as wildlife habitat; and 5) direct and synthetic (i.e., multivariate) ecosystem responses, such as sensitive or indicator target species' population size and demography, habitat-specific biodiversity, standing biomass, productivity, cover, decomposition rate, ecological efficiency, and other metrics of habitat quality. The model should be organized so it eventually provides quantitative predictions about the outcomes. In systems with much empirical data, hindcasting of monitored target species responses provides a useful exercise before forecasting (De Young et al. 2004); however, lengthy monitoring records are rarely available for springs ecosystems or biota. Model outputs are most likely to involve spatial-temporal landscape patterns (e.g., microhabitat area and condition changes through time) as these essential outputs and apply to most of the anticipated response variables; however, many springs exist in settings, such as on cliff faces that may not be detected on aerial photographs and are difficult to survey. Therefore, monitoring of some springs may be challenging.

A Case Study in Conceptual Modeling: The Colorado River in Grand Canyon

One of the most successful recent hydrologically-based and aquatic-terrestrial conceptual ecosystem model is that of Walters et al. (2000). They used a comprehensive ecosystem modeling approach to screen policy options for Colorado River ecosystem management downstream from Glen Canyon Dam. A decade of research and monitoring data were compiled by the Bureau of Reclamation, but had not been synthesized. The policy options under question ranged from changes in hourly variation in stream discharge to major dam modifications, such as improving river-water temperature and turbidity regimes, which were extremely expensive ecosystem management options. The Colorado River model incorporated the existing data, and made fairly accurate predictions about some components of ecosystem responses to policy changes (e.g., autochthonous primary production, insect communities, rainbow trout population). However, and most importantly, it revealed significant uncertainties about several critical resources (e.g., long-term sediment storage, responses of native fishes to physical habitat restoration). Those analyses indicated that data collected using the existing monitoring program were inadequate to detect responses in key resources short of wholesale habitat alteration. As a result, the U.S. Geological Survey and the Bureau of Reclamation have designed and implemented a new, more efficient fisheries monitoring program.

Limitations of Springs Ecosystem Conceptual Modeling

Several factors limit our ability to conceptually model springs ecosystems. 1) Springs ecosystem ecology is highly multidisciplinary involving historical and structural geology and stratigraphy, groundwater and surface-water hydrology, paleontology, climate change, cave biology, lentic and lotic limnology, many of the biological disciplines, as well as archeology, anthropology, contemporary socioeconomics, water law, and conservation sciences; however, integration of ecosystem thought is rarely achieved among these disciplines. 2) Fundamental geophysical and biological information are rarely available for springs. The issue of empirical limitation is particularly relevant to springs where, although considerable ecological conceptualization is possible from studies of lentic and lotic aquatic ecology and riparian ecosystems, few data actually derived from springs are available to support construction of conceptual ecosystem modeling. Information on productivity and decomposition gradients, microbial processes, and invertebrate populations and their ecological roles at springs is particularly weak (Table 1). 3) Springs ecosystem research has been obfuscated by the lack of a comprehensive classification scheme through which we can begin to inventory and map the variety of springs (Springer et al. in prep.). At least 11 types of springs have been documented on the Colorado Plateau thus far: cave, limnocrene, rheocrene, gushet, mound-form, helocrene, hillslope, hanging garden, geyser (geothermal), fountain (non-geothermal), and hypocrene (Table 2; Springer et al. in prep.). 4) Springs ecosystems often are highly dynamic, varying by sphere of discharge or springs type (Table 2; Springer et al. in prep.). They are complex mosaics of complex microhabitats, potentially including at least 13 discrete microhabitats (Table 2; Springer et al. in prep.): cave, orifice, hyporheic, wet wall, madicolous, spray zone, open-water pool, springs stream, low and hill-slope wetlands, riparian, adjacent dry rock, and adjacent linked uplands microhabitats.

The keystone nature of springs ecosystems means that adjacent upland habitats are also ecologically associated with springs, but such linkages remain unstudied. Springs microhabitat mosaics are variably affected by complex subterranean and surface-flow processes, water quality, geomorphology, positional conditions (elevation, aspect, dip angle), biological processes and interactions, and anthropogenic impacts, generally in a bottom-up trophic fashion. Large uncertainties around complex interactions across trophic levels abound in ecosystem modeling research (Walters et al. 2000, De Young et al. 2004). For example, soil invertebrates may influence litter decomposition, affecting both soil development and future productivity (e.g., Douce and Webb 1978). Such terrestrial interactions have yet to be considered at springs, but may be fundamentally important to ecosystem integrity. A further complicating factor is the lack of available experimental sites with large, multiple springs sources for testing basic concepts in springs ecosystem theory. River ecology is conceptually well-grounded in the river continuum concept and its associated paradigms (Vannote et al. 1980; Stevens et al. 1997b). However, the complex data and diverse trees of knowledge requiring integration into a coherent conceptual theoretical framework of springs ecosystem ecology make this a particularly difficult forest to see.

Table 1: Relative quality of biological information for springs (or analogous aquatic/riparian) microhabitats on the Colorado Plateau, based on review of existing literature and unpublished observations by the authors. Categories of data quality are: no data to poor = *, poor = **, moderate = ***, good = ****, and excellent = *****.

Habitat	Biota	Species Richness	Species Density	Soil/Habitat Relations	Nutrient/Food Requirements	Food Web Relations	Productivity (g/C/m2/yr)	Successional Rate	Biogeography	Basic Life History	Quality of Inventory
Orifice	Periphyton	*	*	*	*	*	*	*	*	*	*
	Vegetation	***	*	***	*	*	*	*	***	***	*
	Invertebrates	*	*	***	*	*	*	*	***	*	*
	Vertebrates	*	*	****	***	*	*	*	****	****	*
Backwall	Periphyton	*	*	*	*	*	*	*	*	*	*
	Vegetation	****	*	***	*	*	*	*	****	***	***
	Invertebrates	***	*	***	*	*	*	*	***	***	*
	Vertebrates	***	*	****	***	***	*	*	*****	*****	*
Open-water pool	Periphyton	*	*	***	*	***	*	*	*	*	*
	Vegetation	***	*	***	***	***	*	*	****	****	***
	Invertebrates	***	*	***	***	*	*	*	*	***	*
	Vertebrates	***	*	****	***	***	*	*	*****	*****	*
Madicolous	Periphyton	**	*	**	**	*	**	*	*	**	*
	Vegetation	****	*	**	***	**	**	**	**	***	**
	Invertebrates	***	*	***	***	***	**	***	**	****	***
	Vertebrates	***	*	n/a	***	***	**	**	***	****	***
Spring stream	Periphyton	*	*	*	*	***	***	***	*	*	*
	Vegetation	****	*	***	***	***	****	***	*****	****	***
	Invertebrates	***	***	***	***	***	*	***	***	***	*
	Vertebrates	****	*	****	***	****	*	*	*****	*****	***
Wetlands	Periphyton	*	*	*	***	***	***	*	*	*	*

Habitat	Biota	Species Richness	Species Density	Soil/Habitat Relations	Nutrient/Food Requirements	Food Web Relations	Productivity (g/C/m2/yr)	Successional Rate	Biogeography	Basic Life History	Quality of Inventory
	Vegetation	****	***	****	***	***	***	***	*****	*****	***
	Invertebrates	***	*	***	*	*	*	*	***	***	*
	Vertebrates	****	*	****	***	****	****	*	*****	*****	***
Riparian	Periphyton	*	*	*	*	*	*	*	*	*	*
	Vegetation	****	***	****	***	***	***	***	*****	*****	***
	Invertebrates	***	***	***	*	*	*	*	***	***	*
	Vertebrates	****	***	****	***	****	****	***	*****	*****	***
Uplands	Periphyton	*	*	*	*	*	*	*	*	*	*
	Vegetation	****	***	****	***	***	****	***	*****	*****	***
	Invertebrates	***	***	***	*	*	*	*	***	***	*
	Vertebrates	****	***	****	***	****	****	***	*****	*****	***

Table 2: Estimated likelihood of occurrence of 13 springs microhabitats at 11 terrestrial springs types reported on the Colorado Plateau (data from Springer et al. in prep. and LES unpublished observations). Occurrence likelihood: 0 – microhabit does not occur at a springs type, 1 – very low likelihood of occurrence, 2 – low likelihood, 3 – moderate likelihood, 4 – fair likelihood, 5 – high likelihood of occurrence at that springs type. Spring types: cave = emerges in cave; limnocrene = emerges in pool; rheocrene = flowing into stream channel; gushet = discrete source gushes from bedrock; mound-form = emerges from mineralized mound; helocrene = emerges from low gradient wet meadow; hillslope = emerges from hillslope; hanging garden = dripping flow, generally horizontal emergence; geyser = explosive flow; fountain = artesian fountain; hypocrene = buried spring, no surface flow.

Spring Type	Springs Habitats													Mean Microhabitat Diversity of a Springs Type
	Cave Interior	**Orifice**	**Hyporheic**	**Wet Wall**	**Madicolous**	**Spray Zone**	**Open-water pool**	**Spring Stream**	**Low-slope Wetlands**	**Hillslope Wet Meadow**	**Riparian**	**Adjacent Dry Rock**	**Adjacent Uplands Linkage**	
Cave	5	1	2	5	3	1	5	5				5	5	3.70
Limnocrene	1	5	3	1	1	1	5	5	3	1	5	3	5	3.00
Rheocrene	3	5	3	3	3	3	4	5	4	1	5	5	5	3.77
Gushet	4	5	3	3	3	3	4	5	4	3	5	5	5	4.00
Mound-form	1	5	2	3	3	1	4	5	3	1	3	5	3	3.00
Helocrene	1	2	3	2	2	1	3	3	5	3	5	2	5	2.85
Hillslope	1	2	3	2	2	1	3	3	4	5	5	3	5	3.00
Hanging garden	1	3	2	5	3	4	5	5	2	4	5	5	5	3.77
Geyser	1	5	2	3	3	3	3	4	3	1	3	5	3	3.00
Fountain	1	5	2	3	3	3	3	5	3	3	4	5	5	3.46
Hypocrene	1		1						3	4	4	5	5	3.29
Mean Microhabitat Frequency Across Springs Types	1.82	3.80	2.36	3.00	2.60	2.10	3.90	4.50	3.40	2.60	4.40	4.36	4.64	3.35

Conceptual model design

Model Overview

The springs ecosystem conceptual model consists of a controls model coupled with a stressors model (*sensu* Gross 2003; Fig. 1). The controls model involves eight linked static/descriptive, probabilistic, and/or dynamics submodels that govern natural ecosystem function and features of terrestrial springs in a physical, "bottom-up" fashion (Fig. 2). We emphasize the importance of "bottom-up" physical controls on components and processes that create the habitat templates on which trophically linked springs assemblages develop. Although we do not discount "top-down" trophic cascade effects on springs ecosystem structure, we have yet to observe such phenomena over-riding physical, bottom-up controls at springs. The stressors model summarizes anthropogenic stressors, and presents an analysis of the human impacts, interactions, and thresholds that affect the ecosystem characteristics and processes in the controls model. The major human stressors of each of the eight submodels are described, discussed, and analyzed using a relative impact index based on our observations of the distribution and function of microhabitats at different types of undisturbed springs on the Colorado Plateau. A thorough analysis is warranted when more data have been compiled.

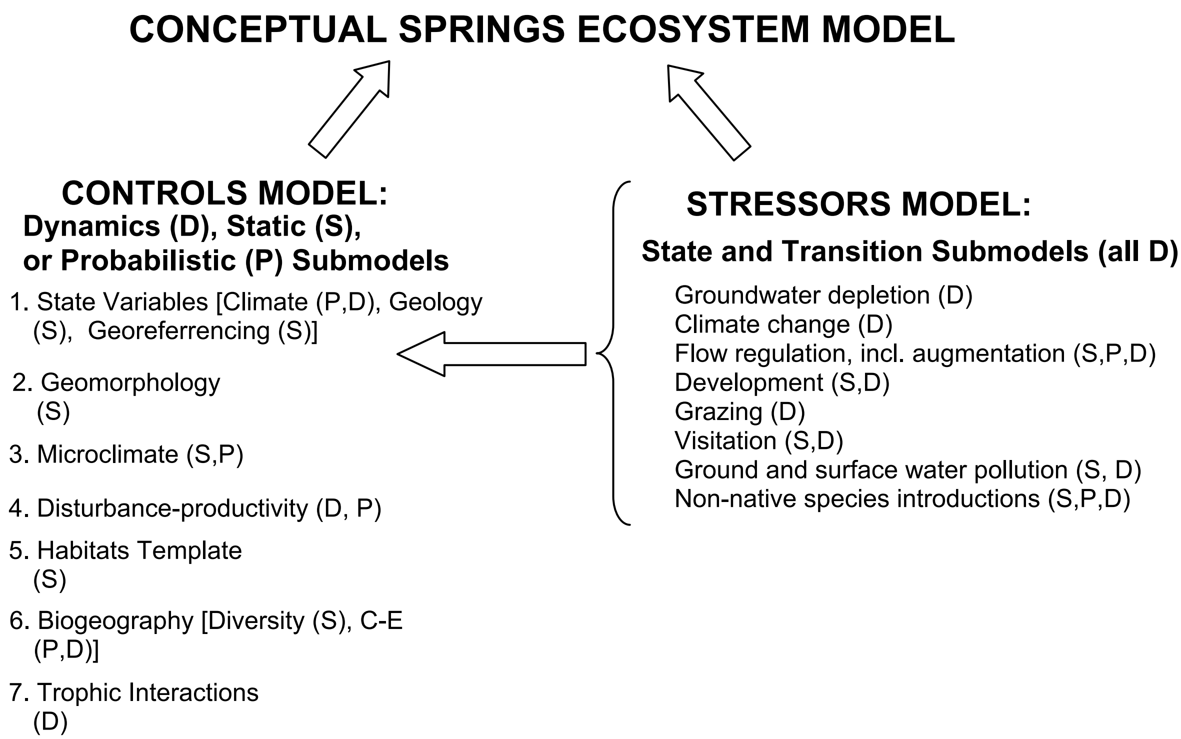


Fig. 1: Design of the conceptual springs ecosystem model as a controls and stressors model couplet . Submodel types: D – dynamic response process submodel, P – probabilistic phenomena, S –static, descriptive submodels.

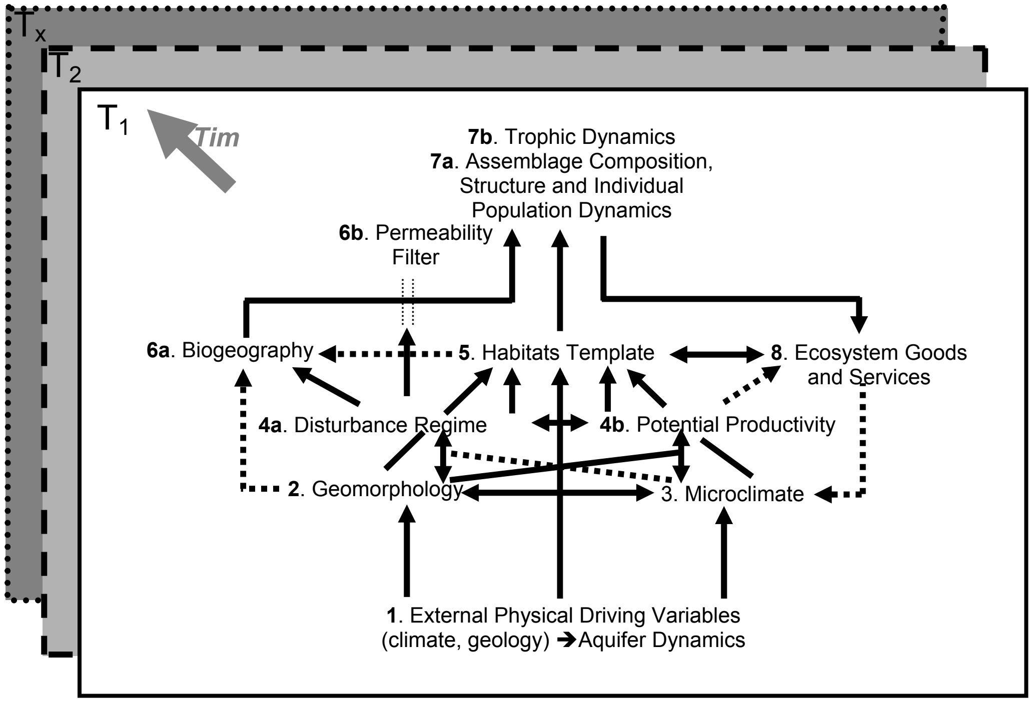


Fig. 2: General springs ecosystem model, showing the interactions among the submodels described in the text. T_1-T_X is time 1 through future time x. ADS is the assemblage development status filter submodel. Solid lines represent strong, direct ecological effects, while dotted lines indicate indirect effects

Organization of the Controls Model

The controls model portion of this springs ecosystem conceptual model includes eight submodels that capture the factors and processes most strongly influencing natural ecosystem structure, function, and temporal change (Table 3). The first four submodels are inter-related, each affected by several physical driving variables and their interactions. Collectively, they generate a template of at least 13 major microhabitats associated with the ≥11 types of springs found on the Colorado Plateau (Table 2). The applicability of each submodel may vary according to spring type, but all are likely applicable to some extent at each springs. All submodels are likely to be modified by anthropogenic activities. The eight submodels in the controls model include the following:

1) The aquifer dynamics submodel describes interactions between regional climate and geology, which collectively result in the springs' emergence at a given location with characteristic hydrogeochemical and flow patterns.
2) The geomorphology submodel relates the geologic context to microtopography and the geomorphology of the orifice and first 100 m of the runout stream, as well as the regional extent of isolation of one spring from others.
3) The microclimate submodel links the state variables of geology and regional climate through the geomorphology submodel to describe the thermal, humidity, solar radiation, and potential evapotranspiration (PET) regimes of the springs orifice and runout stream.
4) The disturbance-productivity submodel is a hinge point in this suite of physical driver conceptual submodels. Arising from interactions of the above three submodels, natural disturbance and potential productivity exert powerful impacts on ecosystem structure and function. This submodel relates geomorphology, regional climate, and microclimate to describe the probability of natural physical disturbance (e.g., flooding, rockfall, fire) and the potential productivity of the orifice and runout stream.

5) Together, the above four submodels dynamically produce a mosaic of 13 potential microhabitats at and around the springs orifice, on which springs assemblages develop over ecological and evolutionary time
6) Species colonize and persist in springs ecosystems as a result of multi-scale biogeographic processes, and such processes regulate species diversity and ecosystem structure and function.
7) The trophic dynamics submodel describes interactions among the springs' biota, some of which feedback to ecosystem structure and function through assemblage composition, structure, and developmental feedback, and trophic dynamics, including ecological efficiency and resilience to disturbance.
8) Springs ecosystems provide an array of ecosystem goods and services in relation to the keystone ecosystem function of the springs in the overall landscape. These processes provide feedback to microclimate and microhabitat development, and provide commodities to wildlife and humans (e.g., water, fuel wood, wildlife, wildlife habitat, recreation values). In addition to physical products, some ecosystem features are useful as monitoring indicators or of importance as non-use values.

Table 3: Terrestrial springs physical, habitat and biological dynamics submodels. State (ultimate, sometimes indirect) and proximal (immediate, direct) model driving components. Each submodel incorporates temporal rates of change.

No.	Submodel	Model Components (Drivers)	Interaction Functions / Processes	Submodel Outputs	Ecosystem Responses
1	***State variables: aquifer/groundwater dynamics***	State (ultimate) variables: regional climate; aquifer and orifice bedrock geology; geologic structure; elevation; latitude; longitude	Hydrostatic head pressure; climate-aquifer relationships involving recharge and discharge; storage; geochemical evolution of groundwater; rock hardness and solubility; fracture patterns	Water table dynamics; springs emergence and distribution within the landscape; water quality; local geomorphology; micro-climate(s), and hydrography	Springs flow and WQ variability; aquatic, wetland, and riparian habitat development; Feedback to rockfall disturbance frequency
2	***Geomorphology***	Proximal variables: springs density; microsite geomorphic configuration of the orifice and runout stream; water and soil geochemistry; local hydrology (i.e., hydrography, stage–to-discharge relationships, flood frequency); rockfall or other disturbance frequencies State variables: geology, landforms, climate, latitude, longitude, elevation	Geomorphic development; microclimate feedback; soil formation; disturbance regime characteristics; erosion and sediment transport; sub-flood flow dynamics;	Habitat development through natural disturbances; wetted area; open colonization (niche) space	Potential productivity and organic matter accumulation; aquatic, wetland, and riparian plant recruitment;
3	***Microclimate***	Potential solar radiation State variables: climate, elevation, latitude, longitude, geomorphology	Solar radiation flux; freeze-thaw cycles; seasonal variation in temperature, relative humidity, soil moisture	Potential evapo-transpiration (local model); thermal, humidity, soil moisture regime; growing season duration	Thermal and humidity regimes; refugia; levels of PET and terrestrial diversity
4	***Disturbance/ productivity***	Geomorphic configuration of site, flood frequency in adjacent streams, growth rate State variables: geology, climate and microclimate, channel geometry, flows, geomorphology	Flooding, rockfall, drought, stream power, evapotranspiration, growth period; competitive interactions among plants	Killing events that eliminate established individuals and open habitat (in which germination occurs); habitat structure	Potential productivity; endemism to dynamic assemblages of flora and fauna; vegetation structure

No.	Submodel	Model Components (Drivers)	Functions / Processes	Submodel Outputs	Ecosystem Responses
5	***Habitat mosaic***	Geomorphology of the orifice and runout stream, microclimate, disturbance regime, potential productivity State variables: geology, climate, aquifer	Habitat development and interactions	Potential and dynamic habitat area, vegetation cover development, trophic development	Colonizable microhabitats
6	***Biogeography***	Potential biodiversity; dispersal, colonization, and extirpation probabilities; disturbance intensity, productivity State variables: species pool, springs and habitat patch distribution, habitat configuration, climate, geology	Disturbance – productivity dynamics, species dispersal, migration, colonization, extirpation / extinction	Colonization, assemblage composition, proportion of weedy versus endemic or rare taxa	Assemblage composition
7	***Trophic structure***	Competition, predation, parasitism, site assemblage history (sorting) State variables: climate, elevation, aspect, water chemistry	Nutrient spiraling; age-specific population dynamics; predator- prey relationships, competition, parasitism interactions	Species diversity, population and assemblage structure; trophic complexity; biomass; ecological efficiency	Springs ecosystem characteristics, flow, and biological products
8	***Ecosystem goods and services***	Products of trophic structure Submodel 7 State variables: controls submodels 1-6	Organic production and exploitation; nutrient capture; feedback into Submodels 3, 5, 7	Flow; water quality; organic production; harvestable biota; feedback regulation of habitat quality; monitoring variables; ecosystem health	Balanced ecosystem energetics

Organization of the Stressors Model

The controls model is, in turn, influenced by an ecosystem stressors model that includes a large array of anthropogenic state-transitions (Fig. 1). The overall stressors model describes human impacts and interactions, which affect virtually all of the ecosystem features, components and processes described in the controls model, but in a hierarchical fashion. Anthropogenic impacts that affect state driving variables exert the most severe and least manageable impacts on ecosystems, and although impacts higher up the ecosystem structure (i.e., grazing impacts on vegetation) may also be severe, such impacts may be rectified through management. The stressors model is described through a state-transition framework that identifies probable consequences of threshold or dosage-dependent treatment effects. Contemporary anthropogenic stressors, such as ground water withdrawal or pollution affect virtually all components and processes in each submodel in the ecosystem and are overlaid on the natural ecosystem development or condition, typically reducing or eliminating ecological function.

Humans have a long history of springs ecosystems use. Haynes (in prep.) documents extensive human use of springs in North America as hunting sites at least since the Pleistocene. Few springs on the Colorado Plateau, and probably no large springs in Europe, Asia, Africa, or Australia have been free from human impacts during late Pleistocene or Holocene time. Therefore, relegation of human impacts to secondary roles in springs ecosystem ecology somewhat distorts this long-term relationship. Nevertheless, we describe several anthropogenic stressor submodels in detail, emphasizing the drivers, interactions, and range of potential outcomes. These stressor submodels serve as examples, rather than the full range, of human impacts on springs -- a topic which is beyond the scope of this document.

Controls Model Components

Aquifer Dynamics –State Variables Submodel 1

Overview: Climate, geology, and their interactions are state variables that exert primary control over aquifer configuration and dynamics. In combination, these variables control the emergence or exposure of water at or near the surface at a given location with characteristic hydrogeochemical and flow patterns and microhabitats (Figs. 2,3; Tables 2, 3). At the largest spatial scale, geologic processes control the development of drainage basins. The geologic setting of the aquifer involves a spatial description of the stratigraphy and geologic structure, and a mechanistic description of porosity of the groundwater basin's soils and bedrock. Regional climate probabilistically approximates the precipitation or storm events over durations relevant to the residence time of groundwater in the basin and flooding in basins. Therefore, we emphasize aquifer modeling as the primary physical driver of ecosystem processes because aquifers integrate geo-climatic factors and their interactions at local basin or larger spatial scales and produce the characteristic patterns of springs discharge and water chemistry.

State (Physical) Driving Variables: Aquifers of the Colorado Plateau often exist in the context of multiple conformably stacked strata dating from Precambrian to Holocene time (Fig. 3). Colorado Plateau latitudes ranges from 33^{o} to 43^{o} N and longitude ranges from approximately 106 to 113^{o} W. Latitude and longitude affect storm type and frequency on the Plateau, with the southern Plateau having a bimodal precipitation pattern that weakens somewhat to the north. Meteoric precipitation sources infiltrate variably permeable or fractured strata, and groundwater flow paths and retention times may range in length from very short to extremely long (potentially hundreds of km and thousands of years). These meteoric sources include snowmelt at the highest elevations, summer and winter rainstorms at middle and high elevations, and summer storms at middle and low elevations. Given this complexity, the aquifer/groundwater dynamics submodel must address relationships between climate and aquifer dynamics to the source, quality, and flow of springs, on which many other attributes of springs ecosystem rely.

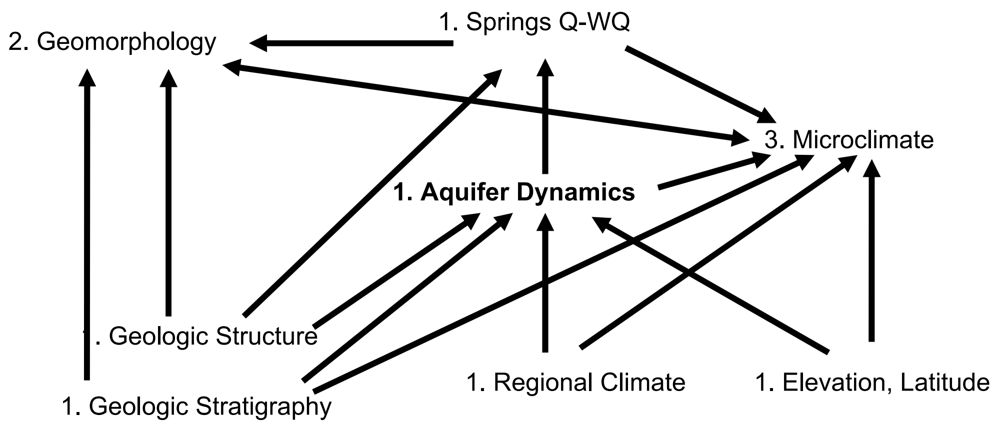


Fig. 3: Aquifer dynamics, as influenced by external physical driving variables and interactions, in relation to adjacent springs ecosystem model components, including the geomorphology (2) and microclimate (3) submodels.

The aquifer/groundwater dynamics submodel (Fig. 3) applies thresholds to the conceptual ecosystem model. These thresholds depend on the variability of spring discharge, the trends in timing and magnitude of spring discharge, and the depth to saturated rock/soil. For example, riparian vegetation has thresholds of available depths to water for recruitment and for maintenance conditions (Springer et al. 1999). Typically, depth to groundwater must be at land surface for recruitment and must not exceed the rooting depth of the colonizing plant species for maintenance. This threshold depth may have a natural diurnal, seasonal, or annual variability, which influences the function of the associated ecosystem. Most aquatic species require perennial flow. Any disruption to perennial flow of the springs due to groundwater pumping, or reduction in recharge from climate, even if only for part of the year, may be detrimental to the ecosystem.

The first step of the aquifer dynamics submodel involves the creation of a conceptual groundwater flow model. This model is generally a pictorial representation. It is frequently in the form of a simplified diagram or a hydrogeologic cross section (Anderson and Woessner 1992; e.g., Fig. 4). A conceptual groundwater flow model forces the modeler to simplify and organize all available data through the following major steps; (1) define the hydrostratigraphic units, (2) prepare a conceptual water budget, and (3) define the groundwater flow system. Because most spring systems lack data for many of the details necessary to construct a detailed conceptual model, the modeler must rely on the available data and the local/regional hydrogeologic literature.

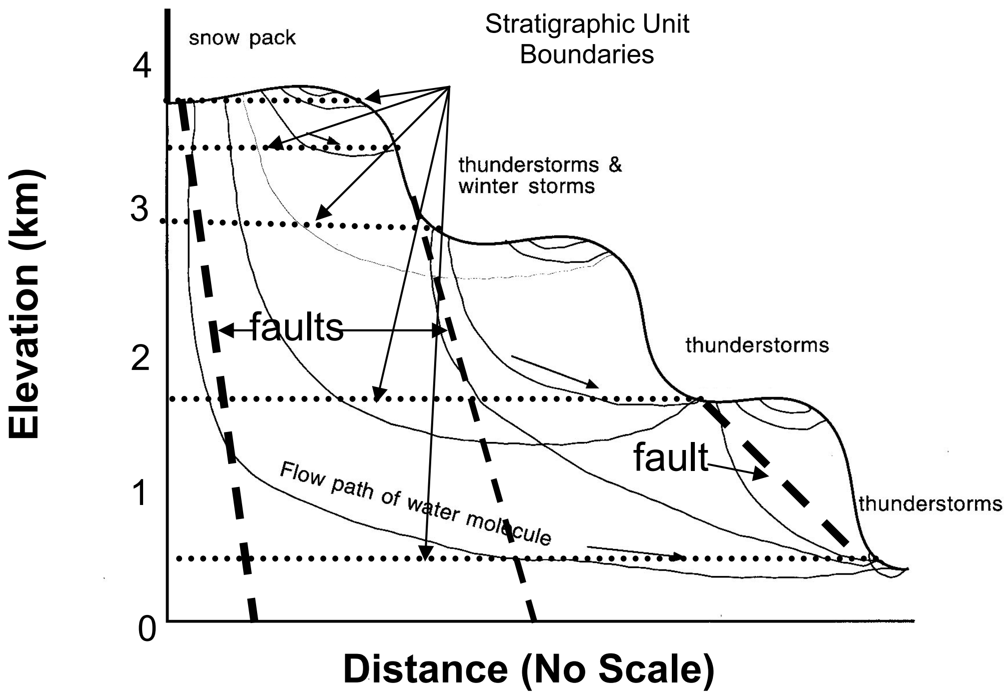


Fig. 4: General configuration of meteoric source areas, aquifer recharge sources, flow pathways, and springs on the Colorado Plateau (modified from GCWC 2002).

Definition of the hydrostratigraphic unit is part of the inventory and assessment program for springs ecosystems. Likely this information will only be based on an accurate description of the geologic unit which outcrops where the spring discharges. If available, subsurface data from interpreted well logs or geophysical data can be used to help define the hydrostratigraphic unit. The description of the hydrostratigraphic unit should include any known spatial variability of the unit such as the distribution of faults, fractures, facies changes, or changes in thicknesses of the unit.

A conceptual water budget describes all of the sources of water into and out of the aquifer and any changes of storage within the aquifer. Typical sources for water into the system include precipitation (rain or snow melt), underflow from adjoining aquifers, or recharge from well, lagoons, septic tanks, or other sources. Typical sources for water out of the flow system include natural groundwater discharge (spring flow, stream baseflow, and leakage to under/overlying units), evapotranspiration (ET), or groundwater withdrawal (pumping). A difficulty with the conceptual water budget is to describe the change in flow with time. Some springs have remarkably constant discharge, but many do not. The modeler must determine which flow conditions are critical for the ecosystem model. For example, summer low flow may be most important to sustain certain species, snow melt high flow may be important as a disturbance factor, or winter baseflow might be most important to understand the stability of flow from the spring.

Model Outputs - Springs Discharge: The flow system must be defined by determining where the water flows, how fast it flows, and the age (residence time) of emerging water. The information to answer these questions is part of the data collected with the field protocols and is determined in our proposed classification system. The locations and types of recharge to the system can be determined from geochemical data (i.e. ^{18}O and ^{2}H isotopes). If any wells exist in the aquifer upgradient of the spring, water levels can be measured and hydraulic gradients calculated. When hydraulic gradients are coupled with estimates of hydraulic conductivity for the aquifers, an estimate of the velocity of the water and subsequently the age of the water can be estimated. Because specific hydraulic conductivity measurements are rare, estimates of hydraulic conductivity from equivalent units cited in the literature are normally used with estimation of ranges of uncertainty.

The capture zone for a spring is the three-dimensional subsurface region of the aquifer captured by discharge of the spring and projected in a two-dimensional shape on a map. Capture zones were delineated for springs of the South Rim of the Grand Canyon by Kessler (2002) based on a time-of-travel criteria with a numerical groundwater flow model. Although capture zones may be described with a number of different techniques (Springer 1990), probably the most appropriate capture zone delineation techniques for springs are hydrogeological mapping or numerical flow modeling. Because numerical flow modeling is beyond the scope of available data and resources for most springs on the Colorado Plateau, hydrogeological mapping will likely be the most feasible technique to delineate capture zones. Hydrogeological mapping delineation of capture zones is generally undertaken after construction of the conceptual groundwater flow model. The hydrogeologic boundaries of the system need to be identified and time-of-travel criteria applied from geochemical or geological information. Typically, simple analytical flow models or more complex numerical flow models are used to develop travel-time related capture zones. Also, numerical flow models are necessary to describe any transient nature of a flow system. Simple hydrogeological mapping can only describe flow under one steady-state condition of an aquifer. If the water budget of a spring is influenced by short- or long-term fluctuations in climate or by the cumulative effects of pumping from wells in the capture zone, then only numerical models are capable of describing the changes.

Numerical groundwater flow models use a series of equations for flow and water budgets to describe water flowing into, through, and out of aquifers (Anderson and Woessner 1992). The most commonly used numerical groundwater flow model is the U.S. Geological Survey's modular, three-dimensional, finite-difference model (MODFLOW, Harbaugh and McDonald 1996). Bredehoeft (2002) discussed the hydrogeologic science necessary to achieve a steady-state condition with these types of models under specific pumping scenarios for an aquifer. Although Bredehoeft (2002) defines the mathematical conditions necessary to maintain a sustainable pumping rate for a well, the new steady-state condition may not sustain biological systems dependent on the virgin discharge from the aquifer. To sustain all physical, biological, and cultural systems depending on an aquifer requires balancing the entire water budget (recharge, discharge, and storage), not just the loss component (Kendy 2003; Molden and Sakthivadivel 1999). Coupled physical and biological models show promise in their ability to describe the conditions necessary for physical systems to sustain biological systems (Springer et al 1999; Fig. 5).

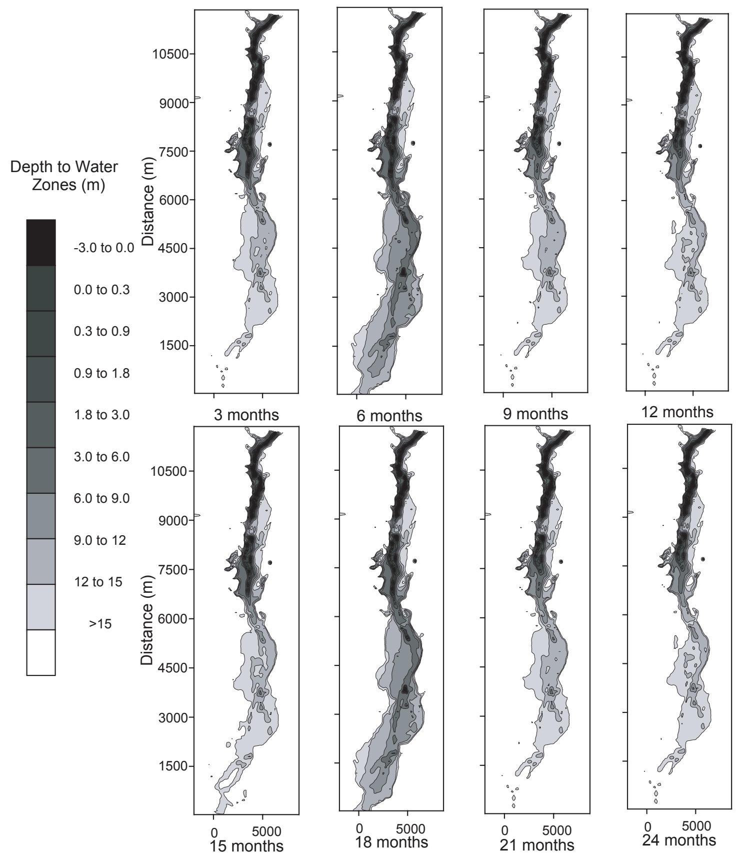


Fig. 5: Time series study by 3-month intervals of depth to water zones for a seasonally varying flow scenario calculated with GIS and numerical flow model (Springer et al. 1999).

Springer et al. (1999) developed a methodology for coupling biotic and abiotic models in a GIS format to evaluate the potential for groundwater recharge and riparian vegetation restoration. Although others developed models to link riparian vegetation to hydrology (Auble et al. 1994; Scott et al. 1997, 1999), those studies have focused on seedling establishment or community composition in relation to surface flows not on depth to groundwater. The presence of relatively high groundwater levels is not the sole physical factor structuring riparian vegetation; however, it is critical for the maintenance of arid riparian communities (Rood and Mahoney 1990; Stromberg et al. 1996; Scott et al. 1993, 1997, 1999; Shafroth et al. 1998). The methodology developed by Springer et al (1999) was applied to a reach of the Agua Fria River, Arizona, below Camp Dyer Diversion Dam, to predict the impacts of a release on the hydrogeologic system and the potential to maintain riparian vegetation once it had been established. The desired outputs were: (1) maps of potential riparian vegetation types based on depth to water; (2) area and ET associated with a vegetation type; (3) area and ET associated with depth to water zones; (4) time series analysis of a monotypic riparian stand; (5) variation in ET volume loss over time; (6) variation in riparian vegetation area (depth to water of approximately 6 m) over time; and (7) an expandable database capable of supporting queries and analyses based on multiple riparian plant species and additional environmental factors.

The limitation for the approach outlined above is the inability of MODFLOW to resolve hydraulic head measurements at the spatial scale of the microhabitats that exist at springs. Springer et al. (1999)

resolved seasonal average hydraulic heads in a large alluvial river channel with average model cell sizes of 100 m x 100 m. This spacing is too coarse for most (if not all) springs on the Colorado Plateau. Kobor (2004) constructed a more spatially refined numerical groundwater model to predict the necessary riparian vegetation maintenance conditions for the channel fed by Cottonwood Spring in the Grand Canyon and resolved daily average hydraulic heads on cells of 0.5 m x 0.5 m.

The types of data necessary to achieve a working aquifer/groundwater dynamics submodel include measurements of water levels from wells (if they exist), long-term precipitation data, well pumping data, springs discharge, wetted areas, material permeability values, and estimates of plant water use and evaporation. In lieu of constructing a well-constrained numerical flow model, a simple conceptual model can be constructed for a poorly constrained springs with some inferences about how the water budget responds to human, climatic, and biotic demands on the water. The only types of data not collected with our proposed springs inventory and assessment program that are necessary to build the aquifer/groundwater dynamics submodel are water levels and pumping rates from adjacent wells.

Model Outputs - Groundwater Quality: Water temperature and chemistry plays a fundamental role in organizing aquatic invertebrate communities. Despite the vast literature on water quality and aquatic invertebrate interactions (reviewed by Merrit and Cummins 1996), springs biotic responses to water quality has not received such attention. A few generalizations can be made about groundwater quality impacts on aquatic and riparian biota, as follows. At highly mineralized springs, biodiversity is likely to be reduced at springs with total dissolved solids (TDS) concentrations of >1000 mg/L. Upper water temperature is widely known to influence biodiversity, and fresh, non-geothermal waters >30^{o}C have reduced biodiversity, although some species are specifically adapted to high water temperatures.

Groundwater quality contributes to the relative environmental constancy and harshness of springs ecosystems, as well as their ecological development. Although not yet modeled in detail, environmental harshness plays a strong role in adaptational endemism. Many examples of endemic aquatic *Pyrgulopsis* and *Trionia* snails, naucorid water bugs, elmid beetles, and *Cyprinodon* pupfish are known from Basin and Range springs (Hershler 1994, Hershler et al. 1999, Hershler and Sada 2002, Polhemus and Polhemus 2002), and complex ecosystems often develop in perennially harsh ecosystems (Blinn in prep.). In contrast to unique southwestern springs vascular plants, which appear to be primarily relictual taxa, endemic invertebrates appear to develop through adaptation to these harsh, constant environments.

Ecosystem Consequences: The aquifer dynamics submodel integrates climate and geology to interactively produce patterned discharge and water quality at the springs orifice. Flow is likely to have a strong dosage-dependent impact on the area and ecological function of the aquatic, wetland and riparian microhabitats associated with a springs (Table 3). Such relationships have been evaluated on some large springs systems (e.g., Grand Canyon Wildlands Council 2004, Hendrickson et al. in prep.). Also, GCWC demonstrated that the aquifer dynamics model can be used to predict biological development in springs runout stream and riparian ecosystems, and that such models have considerable management utility (Fig, 5). However, the features and process operating on the runout stream are only partially controlled by this submodel, and are strongly affected by geomorphic, microclimate, disturbance, and other factors influence surface flow and channel geometry.

Aquifer geochemistry is similarly influenced by interactions between the driving variables and the duration of the flow path. Deep aquifer flow paths may be millenial in duration, generally increasing the ion content of groundwater. With such lengthy flow paths, relatively minor levels of groundwater extraction may permanently dewater springs, causing loss of species and water sources. Well data from various points within a groundwater basin may demonstrate the rate of geochemical transformation. Such information may be useful for dating water, but such studies have not, to our knowledge, been undertaken on the Colorado Plateau.

Geomorphologic Settings and Processes Submodel 2

Drivers: The geomorphology of the springs orifice and the first 100 m of runout stream are affected by interactions between climate, geology, and aquifer dynamics operating at local, synoptic, and regional spatial scales (10^{-6} to $>10^{5}$ km^{2}, depending on the size of the springs ecosystem in relation to the basin;

Table 4). These factors and interactions produce a site-specific geomorphic configuration with temporally and spatially patterned flow and water chemistry at the orifice and also influence geophysical development and microclimate feedback on the springs ecosystem in the landscape (Fig. 6, Table 3). The geomorphic submodel involves several descriptive and probabilistic elements, which are described in Table 4 and hierarchically in the following section.

Table 4: The array and variability of geologic and aquifer variables most strongly affecting the geomorphology and ecosystem development of natural springs on the Colorado Plateau. GW – groundwater. Values for flow are discussed in Springer et al. (in prep.).

Elevation (m)	Aspect	Dip Angle	Water Quality (TDS, mg/L)	Flow (L/s)	GW T (^oC)
350-1200	S	Flat (0^o-10^o)	Low (<500 mg/L)	very small	cold-steady or variable
1200-1800	E	Low (10^o-25^o)	Moderate (500-1000 mg/L)	small	mean annual-steady or variable
1800-2400	W	Medium (25^o-40^o)	High (<1000-2000 mg/L)	medium	warm - steady or variable
2400-3200	N	High (45^o-160)	Extreme (>2000 mg/L)	large	geothermal
>3200		Steep (>60^o)		very large	

Stratigraphy and Structure*:* Geological stratigraphy and structure (particularly the distribution of fracture and geologic contacts) permit groundwater exposure or emergence at the surface and hence the location and position of the orifice. In addition, tectonic factors regulate the local context, dip angle, and aspect of the springs orifice, as well as the groundwater forcing mechanism(s). Although these geological variables are primarily mechanical or descriptive, the distribution of some types of springs types can be predicted by knowing distribution of water-bearing strata, their hydraulic gradients, and the location of canyon- or cliff-forming faults. For example, the distribution of hanging gardens springs emerging from the Navajo Sandstone Formation is reasonably predictable across the Colorado Plateau. This submodel is primarily captured through analyses of mapped stratigraphy and structure within the drainage basin and among adjacent basins.

Elevation*:* Elevation is a tectonically-controlled state variable that plays a significant role in western climate, particularly temperature, precipitation, and the duration of freezing. The adiabatic lapse rate produces approximately 1^oC change/300 m, resulting in the well-known inverse relationship between temperature and higher relative humidity across elevation. Therefore elevation is a strong physical drivers of ecosystem processes and biota. Regional, elevation-related climate, coupled with site aspect strongly affects springs microclimate (Submodel 3), particularly freeze-thaw cyclicity, which may reciprocally affect springs geomorphology.

Elevation also affects many other ecosystem variables. For example, Grand Canyon Wildlands Council (2002) reported few, if any, endemic or rare plant species at springs above 2300 m on the southern Colorado Plateau. It is likely that higher elevations were subject to much shorter growing seasons during the Pleistocene, and there has been insufficient Holocene time to allow endemic speciation to occur at higher elevation springs.

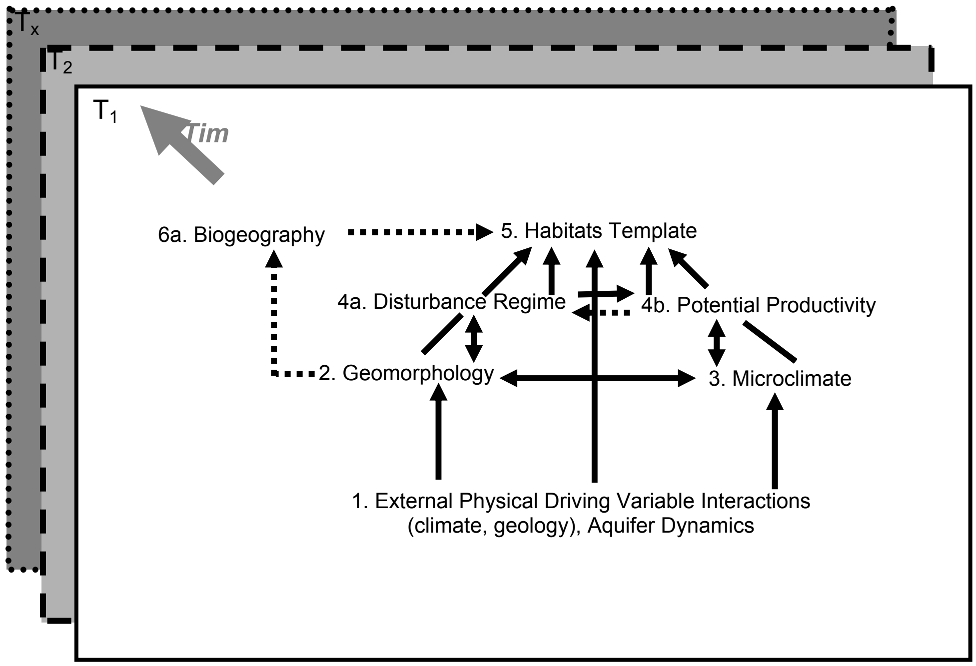


Fig. 6: Springs geomorphic Submodel 2. T_1-T_X – time 1 through future time x. Solid lines represent strong, direct ecological effects, while dotted lines indicate indirect effects.

***Springs Distribution**:* Habitat size and degree of isolation are important determinants of wildlife habitat contiguity, as well as the potential colonizability of springs in a long-term biogeographic context (Submodels 5 and 6, respectively). These characteristics can be described in relation to the distribution and size of neighboring springs using a regional landscape geographic information systems (GIS) analysis. This requires a first order inventory of springs distribution for the basin in question. Although static in nature, anthropogenic reduction of springs density has strongly altered these relationships in some Colorado Plateau settings (Grand Canyon Wildlands Council 2002).

***Geomorphic Configuration of the Springs**:* At the local spatial scale of the springs ecosystem, the landscape and aspect of the orifice environment are static or relatively stable in ecological time. Habitat area measurement, as well as monitoring of spatially explicit variables, at important individual springs will be facilitated by conducting a land survey and developing a triangulated irregular network (TIN) landscape model of the site. A TIN model of the springs requires at least a leveling survey (at small sites, particularly those that are canyon-bound) or, at best, a total station survey. The accuracy of topographic mapping, especially including the elevation of the source, must be accurate to $\leq$1 m to relate the springs discharge to the aquifer dynamics (Submodel 1). In complex terrains, springs mapping cannot be accomplished through photogrammetry because of steep slopes and overhanging walls and sometimes dense vegetation. We recommend conducting the land survey during the winter months, when visibility through the vegetation is increased. The TIN model provides a reliable measurement of the area of the springs and its associated microhabitats, and can serve as an important GIS archival tool to document responses of the springs to anthropogenic and climatic variation. However, development of a site map is relatively costly and time-consuming, and therefore should not be a component of the initial inventory and assessment process, but should be conducted as the first step in monitoring. Monitoring variables should be related to the site base map. Eventually, with a sufficient number of land surveys of springs, quantitative patterns of topography and springs channel geometry may be generalized for different types of springs, as has been accomplished for different stream types (e.g., Rosgen 1996).

Model Outputs: Geomorphology affects most springs ecosystem components and processes, particularly the physical array of habitats. The primary outputs of the geomorphology model include the following: 1) a map of springs distribution in relation to geologic stratrigraphy, structure and elevation in the study area; 2) a GIS analysis of springs distribution (density/km^2 in the landscape, nearest neighbor statistics, patch size statistics); and 3) a TIN model of each springs to be used for long-term monitoring purposes, including physical features such as orifice(s) and prominent rock outcrops, bench marks, site topography, photographic points, channel geometry, and onto which vegetation patches can be mapped.

Ecosystem Consequences: The implications of geomorphic forms and processes on springs vary with respect to the array of springs types and springs microhabitats (Table 2). Slow geomorphic transformation of the springs ecosystem may occur through static and probabilistic processes. Landscape configuration changes slowly at hanging gardens through capillary transport of water into overlying strata. Rock spalls occur through freezing and thawing, increasing the alcove-like geomorphic configuration of these contact springs until the structural limits of the parent bedrock are achieved. Another slow geomorphic change at springs is the gradual growth of springs carbonate mounds. Newly emerged springs may develop increased vegetation cover and a higher decompositional load in comparison with adjacent uplands, resulting in more rapid pedogenesis and increased pH from humic acids. These changes may increase carbonate dissolution of bedrock.

Little recognition presently exists of geomorphic feedback of springs on adjacent landscapes. Geomorphic feedback may involve obvious local-scale development of carbonate mounds or cementation of adjacent channel floors that are more resistant to movement during floods. Also at a local scale, tree stem density may increase at aridlands springs, altering flood-related sediment deposition. At larger scales and over geologic time, it may be that springs alter channel development through increased freeze-thaw and headward erosion, Distinguishing structural control from springs-related influences in this process are likely to be difficult; however, the long-term emergence of springs waters at a given location or from a single fracture system may influence landscape evolution.

<u>Microclimate Submodel 3</u>

Drivers: Springs microclimates are important but poorly quantified ecosystem characteristics that are related to regional climate, local geology, elevation, groundwater temperature, and the configuration and aspect of the orifice in relation to the site's solar radiation budget (Table 5; Fig. 7; Rosenberg et al. 1983). Microclimate is controlled by driving variables of regional and synoptic climate, groundwater temperature, and local geomorphology.

Regional climate is the result of global and continental scale atmospheric and oceanic processes in relation to latitude, longitude, and regional- and continental-scale topography. Regional climate governs general temperature, precipitation, wind speed and direction, cloud cover, storm frequency, general patterns of seasonality, and other variables that affect springs ecosystems and their microclimates. These climate variables are summarized from existing weather station data or regional climate models. At least daily mean, minimum, and maximum values for air temperature, total daily precipitation, and mean and maximum wind speed and direction, as well as growing season length, are needed for modeling relationships to elevation, latitude, and longitude in the study area. The robustness of these relationships depends, of course, on the number of weather stations exist and the duration of coverage in the region. These modeled descriptive relationships can be estimated at any location in the landscape through GIS for any springs of interest, and these variables may be selected for monitoring at important springs reference sites.

Table 5: Springs microclimate variables in relation to spatial scale (local to regional), and effects on ecosystem characteristics.

Scale	Climate and Site Variables	Relationship to ecosystem
Regional climate	Max and min daily temperature	Springs water temperature, vegetation development, spalling rates of backwalls, soil development rate, decomposition rate, etc.
Regional climate	Growing season length (degree-days)	Plant growth and potential site productivity
Regional climate	Precipitation	Potential species distribution, soil development
Regional climate	Mean daily wind speed	Disturbance, PET
Regional climate	Relative humidity	Plant growth and potential site productivity
Regional climate	Potential evapotranspiration	PET rate, primary productivity
Synoptic climate	Latitude, longitude	Storm track relationships
Synoptic climate	Elevation	Modifies regional climate
Local Topography	Aspect	Modifies regional and microclimate by extent and timing of shading; measure effects on solar radiation budget with Solar Pathfinder
Local Topography	Dip angle	Nutrient and materials spiral lengths, soil quality, and moisture retention are inversely related to dip angle.

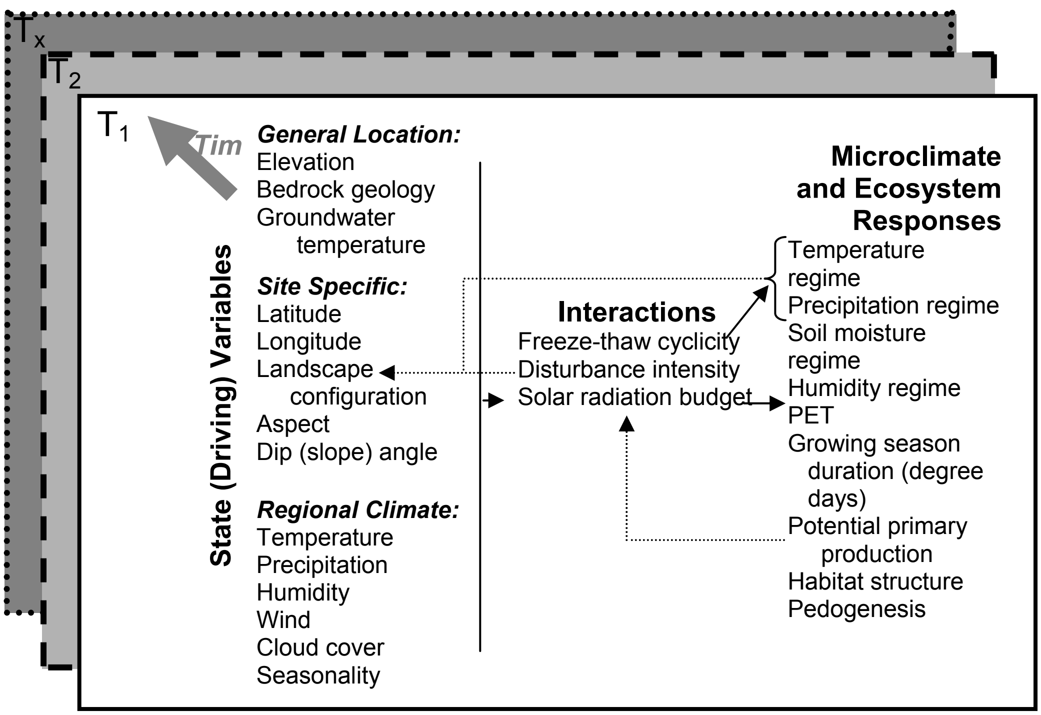


Fig. 7: Springs microclimate Submodel 3, showing interactions between driving and interactions variables, and ecosystem responses. T_1-T_X – time 1 through future time x. Solid lines represent strong, direct ecological effects, dotted lines indicate feedback effects. Disturbance intensity feeds back to local geomorphic configuration of the site.

Geological drivers of microclimate that interact with regional climate include regional geologic stratigraphy and structure (Submodels 1 and 2), which control the local geomorphic configuration of aspect, dip (slope) angle, rock color, and some elements of the emergence environment. Aspect is a geomorphic characteristic of springs that, in topographically diverse terrain, strongly affects ecosystem composition and function. Stevens (unpublished data) found that north-facing slopes in southern Colorado Plateau deserts often receive no direct sunlight during the winter months. North-facing slopes at low elevations on the arid Colorado Plateau are likely to have far more temperate microclimates than are south-facing desert slopes. However, north-facing slopes are likely to be colder and harsher at high elevations, precluding many plant species' survivorship there. Aspect differences in Grand Canyon created climate differences equivalent to an elevation gradient of 700 m between north- and south-facing slopes even though the slopes studied faced each other across a canyon only 200 m wide. As a result of aspect, the two slopes had almost entirely different desert plant communities, with Great Basin Desert species on north-facing slopes and Sonoran Desert species on south-facing slopes.

We present a non-quantitative estimate of aspect impacts on wetland plant diversity on the Colorado Plateau (Fig. 8). This model indicates that south-facing slopes are likely to have higher plant diversity than north-facing sites at high elevations, and that this pattern is reversed at low elevations. Diversity is likely to be higher at intermediate elevations than at lower elevations because salinity and drought stress are negatively related to elevation, and are likely to reduce wetland plant diversity in desert settings. East- and west-facing slopes are likely to support an array of both north- and south-facing species, and therefore east- and west-facing slopes are likely to have higher diversity than south- and north-facing slopes. These conclusions are supported by our analysis of plant diversity across elevation in the Grand Canyon region of the southern Colorado Plateau (Fig. 9, Stevens unpublished data). This analysis demonstrates that both total plant species richness and the diversity of aquatic, wetland, and riparian plant species unimodally peaks at middle elevations on the southern Colorado Plateau. Although more data are needed to refine Fig. 8, the data in Fig. 9 support our general conclusions that wetland plant diversity is likely to be greatest at intermediate elevations.

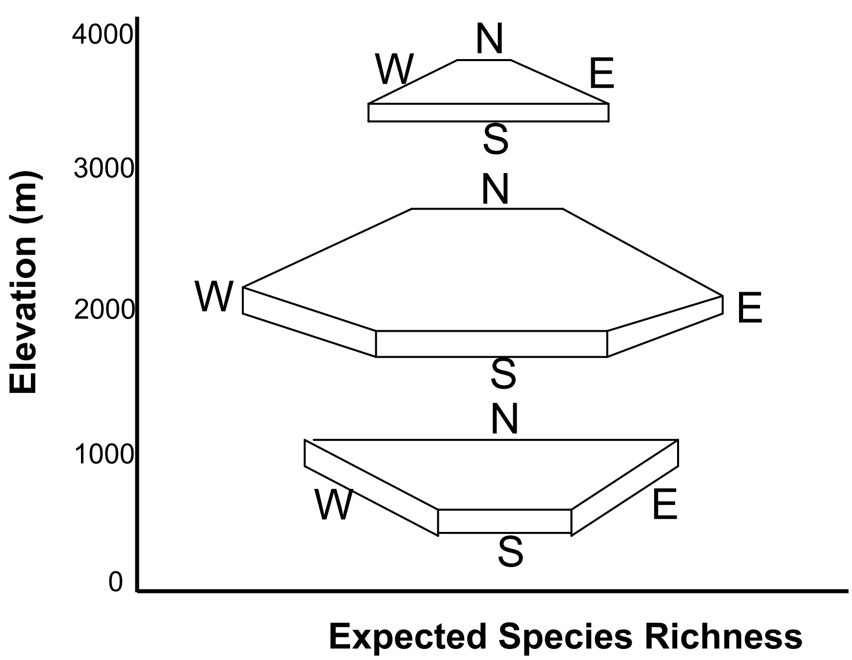


Fig. 8: Predicted species richness (S; no scale) as a function of elevation and aspect. Dip angle is expected to monotonically reduce S.

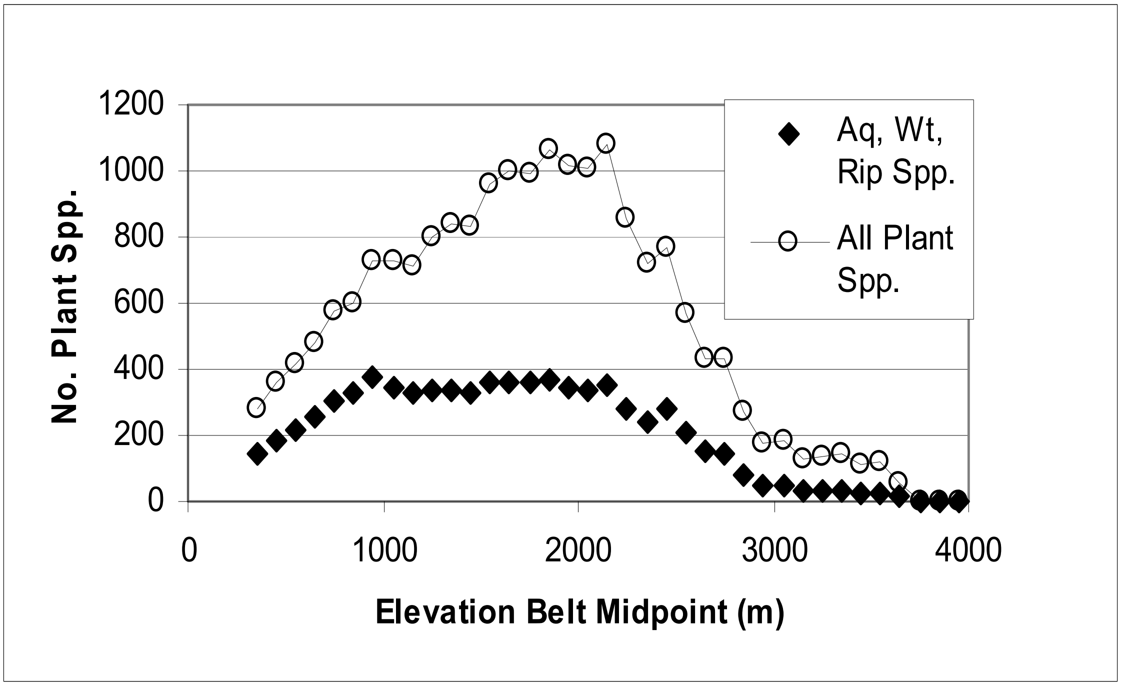


Fig. 9: Number of all higher plant species and number of aquatic, wetland, and riparian plant species by 100 m elevation belts in the Grand Canyon ecoregion, southern Colorado Plateau, Arizona.

Interactions: Interaction effects between regional climate and geomorphology include the site-specific solar energy budget, freeze-thaw cyclicity, and potential evapotranspiration (PET). These are quasi-static, quasi-probabilistic relationships defined by climate interactions with aspect, dip angle, and configuration of the springs with respect to location, geology, and geomorphic features (i.e., cliffs, slopes, elevation, etc.).

Local-scale aspect and the configuration of cliffs and other shading features controls the solar energy budget (solar flux) and hence the amount of ecosystem energy of the springs. The solar energy budget is measured as the mean monthly flux (Mj/mo) or as the percent ambient solar energy received at a site relative to the unobstructed horizon. Solar flux is important to springs because it influences important physical ecosystem properties such as temperature, sunlight availability for photosynthesis, freeze-thaw cyclicity, and the humidity and potential evapotranspiration regime. Solar flux also is affected by interactions among elevation, cloud cover and aerosol concentration, as well as feedback from vegetation development. Solar flux affects primary production and plant growth at springs, generally in a dosage-dependent fashion.

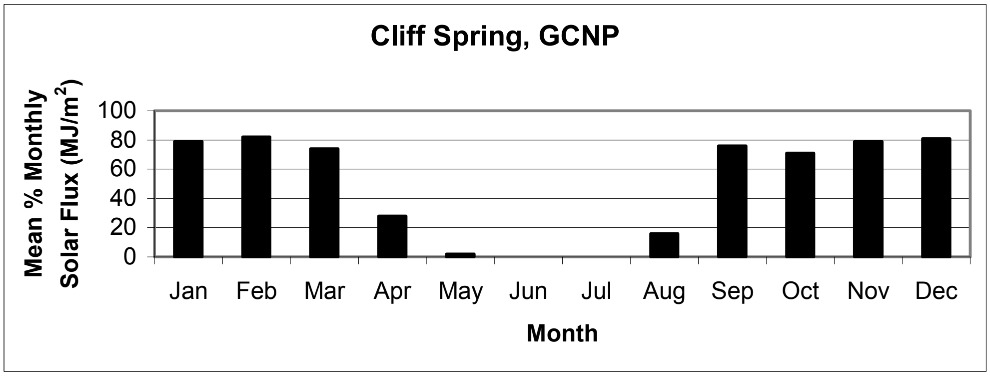
Freeze-thaw cyclicity is a function of regional climate, elevation, aspect, and a springs' local geomorphic configuration. Freeze-thaw cycles affect erosion and rockfall spalling rates as well as many elements of ecosystem form and function. North-facing slopes in the Northern Hemisphere are likely to remain frozen for longer periods of time in the winter; whereas south-facing slopes are likely to undergo freeze-thaw cycles on a daily basis (Stevens unpublished data). This may mean that north-facing sites are less subject to rockfall than are south-facing slopes.

PET is influenced by the thermal and humidity regimes, solar flux, soil moisture availability and variability, and freeze-thaw cyclicity. PET is an ecologically important output of the microclimate submodel because it strongly affects springs vegetation composition and cover, and ecosystem structure and function (Table 4, Fig. 3). While it is possible to estimate relationships among microclimate variables, a regionally specific model is needed for the Colorado Plateau to approximate ranges and variation among these variables and how they influence site-specific PET. Understanding and modeling of local PET at springs is still preliminary (except see Spence 2001). Rowlands (unpublished) modified Thornwaite and Mather's (1957) potential evapotranspiration index, which requires as inputs mean monthly temperature and precipitation, and duration of maximum direct sunlight. With these input variables, such a model may provide an estimate of PET at a specific latitude and elevation on the Colorado Plateau. Spence (2001) used Rowlands (unpublished) PET model to estimate climate conditions at Glen Canyon springs, but the data were insufficient to distinguish the impacts of aspect and other microclimate variables. Although a Colorado Plateau-wide springs microclimate model has yet to be developed, when completed it should relate elevation and aspect-modification of PET and other microclimate variables to springs vegetation composition and cover in a local landscape context.

Ecosystem Responses: Springs microclimates are moderated by interactions among driving and interaction variables, including regional and local geological and geomorphic characteristics, as well as aquifer temperature. Grand Canyon Wildlands Council (2002) quantified the solar radiation budget of Cliff Spring, an east-facing spring at 2280 m elevation on the north rim of Grand Canyon (Fig. 10a). The microclimate of this high elevation hanging gardens springs was strongly modified by its site configuration. It received 70-80 percent of ambient sunlight in the fall and winter, but extensive overhanging cliffs blocked 80-90 percent of the ambient solar radiation in spring and summer when hot dry conditions would otherwise desiccate the springs wet walls. Also, its water temperature (14.3^{o}C) may keep the site somewhat cooler during summer. These conditions were believed responsible for the long-term persistence of a very small population (5 plants) of rare *Primula hunnewellii* on wet cliff faces there.

In another example, Stevens et al. (1997a) reported that Vaseys Paradise Spring, a 0.2 ha spring at 885 m elevation in Grand Canyon, had an east-facing aspect and uniform, moderate temperature (16^{o}C; Fig. 10b). Its relatively warm water temperature buffers it from extremely cold winter temperatures, while its aspect allows the site to warm early on winter days but be cooled by shading from steep adjacent limestone cliffs on hot summer afternoons. These interactions contribute to the support of a high diversity (eight species) of land mollusks, including the lowest known elevation of succineid *Oxyloma* in the Southwest, represented there by the endangered Kanab ambersnail, *O. haydeni kanabensis* (Spamer and Bogan 1994). Again, interactions between aspect, physical features, and aquifer temperature appear to strongly affect microclimate and ecosystem characteristics.

A



B

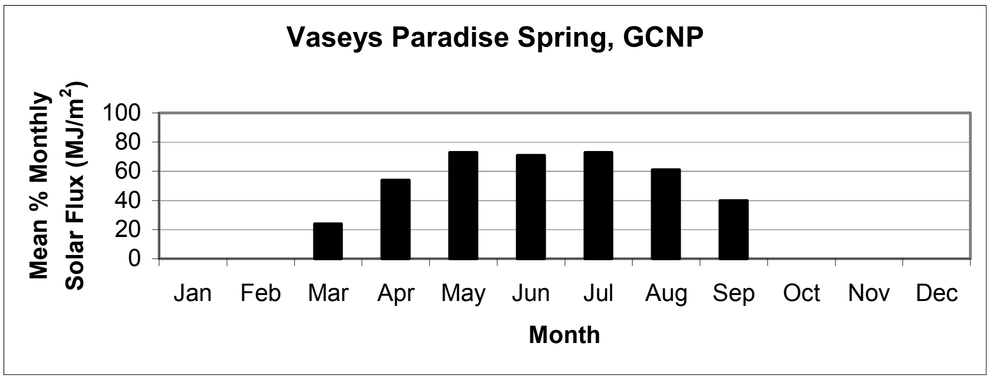


Fig. 10: Mean percent monthly solar radiation flux (MJ/m2) at (A) Cliff Spring and (B) Vaseys Paradise, Grand Canyon National Park, Arizona (data from Grand Canyon Wildlands Council 2002).

Microclimate strongly affects ecosystem structure and function. For example, Holdridge (1947, 1967) and Whittaker (1965, 1970) delineated the distribution of different ecosystem structural types based on thermal, precipitation, and PET data. Soil moisture at southwestern springs is primarily controlled by groundwater rather than precipitation and may not be limiting to vegetation. The thermal and humidity regimes (factors that control PET) are strongly influenced by site configuration and the solar energy budget. When sufficient data are collected across aspect and elevation, the modeling of these variables will allow general estimation of PET and perhaps springs vegetation. In the meantime, case studies may provide some indication of the importance of this kind of research.

Disturbance Intensity-Potential Productivity Submodel 4

Overview: The combined impacts of disturbance intensity and potential productivity affect ecosystem structure in a non-linear fashion (Huston 1979). Flooding and rockfall are probabilistic, precipitation-driven, disturbances with characteristic site-specific frequency, magnitudes, duration, and often predictable seasonal timing. Dynamical drivers of the geomorphic submodel include seasonal variation in precipitation and springs discharge, with geomorphic responses related to scour or burial, sediment deposition, and with impacts extending to variation in the development and composition of vegetation cover. The role of natural disturbance is so powerful in terrestrial springs ecosystems that we consider it to be a fundamental physical driver of post-emergence springs ecosystem development and a hinge point in the overall conceptual ecosystem model. Natural disturbance is commonly defined as a perturbation that alters and exposes habitats to colonization and removes established individuals (Connell 1978, Sousa 1984, Huston 1979). Therefore, disturbance resets ecosystem development and allows change in structure and species composition. Disturbance exists as a probabilistic landscape gradient, creating an array of settings that range from neorefugial (highly disturbed sites, typically dominated by weedy species and recent colonists) to paleorefugial (ecologically stable sites, dominated by long-term resident species, and often endemic genotypes; *sensu* Nekola 1999). Disturbance intensity interacts with potential productivity in a non-linear fashion (Huston 1979).

Potential productivity (measured as the potential g C fixed/m^2/yr) is generated by site geomorphology and the suite of regional- and micro-climate variables discussed above. Productivity also is a powerful determinant of springs ecosystem form and function and interacts with disturbance intensity in a non-linear and non-intuitive fashion. High levels of productivity exist where groundwater levels are at or near the surface or in settings with elevated precipitation and relatively long growing seasons. Low levels of potential productivity exist on barren rock surfaces and cliff faces and in many deserts. In arid regions, potential productivity is generally related to moisture availability. Therefore, desert springs represent an excellent, if not unique, natural laboratory in which to understand the interactive effects of natural disturbance and productivity on biodiversity. The natural disturbance landscape submodel is the direct result of climate-geomorphology interactions, and other natural physical and biological disturbance intensity probabilities (e.g., grazing intensity).

Drivers: The frequency, magnitude, and duration of natural ecological disturbances, or the extent of ecological constancy, profoundly affects post-emergence springs ecosystem development (Table 6, Fig. 11). Common forms of disturbance at Colorado Plateau springs include rapid responses, including flooding and sheetwash during intense precipitation events, rockfall, and fire, as well as slow-acting minor rockfall and chemical precipitation (Table 6). Herbivory is a biogenic form of disturbance and is discussed in Submodel 7 (below).

Flooding: Flooding disturbance strongly and directly affects stream ecosystem development (Table 5). We distinguish between springs that are relatively well-protected from surface flooding (springflow-dominated springs) and those that are regularly flood-disturbed by the associated drainage system into which it discharges (surface-flow dominated springs). However, the geomorphology of spring channels that are relatively unaffected by surface flows has yet to be classified as the methods of Rosgen (1996) do not necessarily apply to non-flood-shaped channels

Table 6: Disturbance factors, geomorphic variables and processes interactively affecting springs ecosystem development.

Factor	Physical Driving Variables	Process(es)	Effects on Ecosystem
Flood disturbance intensity	Channel hydrology dominated by springs flows	Channel-shaping factors in the absence of flooding	Stream channel particle size is unsorted; microhabitat patches small (channel and instream habitat structural diversity variable at fine spatial scale, but lower at coarser scale); substrates relatively stable and pedogenesis may be apparent; decreased diversity unless other disturbance factors are involved; successional state advanced and trajectory stable
	Hydrology dominated by surface channel flows	Surface flow flooding, sediment transport and deposition, streambank erosion, terrace shaping	Stream channel particles are better sorted, creating larger microhabitat patches; channel and instream habitat structure is frequently reorganized; increased plant diversity if disturbance intensity is moderate, decreased if DF is high; successional state "suspended" and trajectory continually reset
Dewatering	Drought or water table drawdown	Surface flow or exposure is interrupted	Seasonal or erratic desiccation of the springs ecosystem eliminates aquatic and wetland functions and components. Reduced aquatic and wetland plant and faunal diversity.
Sheetflow disturbance	Climate (extreme precipitation events)	Sheetflow flooding during extreme rainfall events;	Extreme precipitation events create flow and rockfall disturbance, including sheetflow wash over the tops of adjacent cliffs; resetting slope and channel microhabitats, mortality of spring biota
Rockfall probability	Climate (temperature, precipitation), elevation, aspect interactions	Freeze-thaw cycles; seismic disturbance; other erosional factors	Frequency-related microhabitat adjustment, particularly of backwall microhabitats and spring existing at the base of spall-prone cliffs; may affect diversity if frequency is substantially less than the life span of affected biota
Factor	**Physical Driving Variables**	**Process(es)**	**Effects on Ecosystem**

Geochemical precipitation	Parent rock geology, GW flow path duration, emergent Q and WQ variability	Travertine deposition as carbonate-rich water degasses CO_2 and precipitates $CaCO_3$;	Shapes orifice and in-stream geomorphology, in-stream microhabitats, riparian terraces; process may be affected by microsite algal or bacterial adjustment of pH.
Fire	Geomorphology: dip angle(slope), aspect	Litter accumulation and moisture content, particularly in the adjacent uplands	Killing events, resetting successional dynamics, nutrient release, upland impacts on runout stream water quality

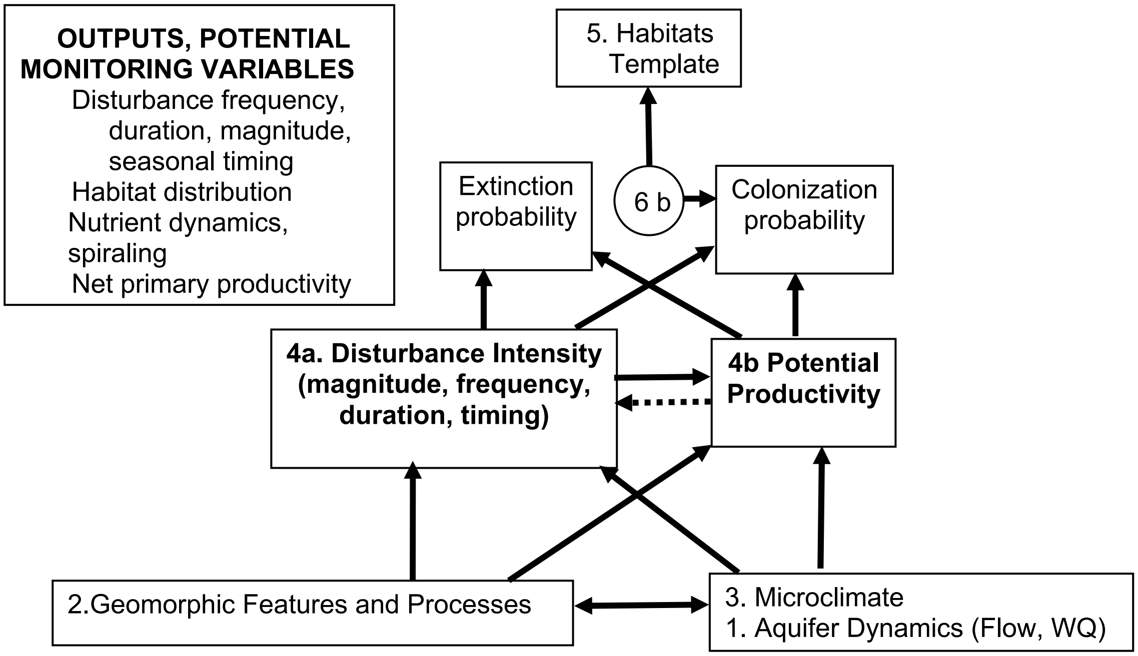


Fig. 11: Relation of the disturbance-productivity submodel to the aquifer dynamics, geomorphology, and microclimate submodels, and its effects on the habitats template and the biogeographic colonization-extinction filter.

In contrast, in surface-flow dominated streams, flooding is widely acknowledged as the largest natural driver affecting ecosystem ecology (Hupp 1988, Junk et al. 1989, Stromberg et al. 1991). Because sediment transport is an exponential function of flow, high flows are responsible for shaping channel geometry in surface-flow dominated streams. Flood frequency is a probabilistic function of storm type distribution, precipitation dynamics, and hydrology. Most stream channels in the topographically diverse terrains of the Colorado Plateau are shaped by several kinds of flooding events including bankfull and higher floods, hyperconcentrated flows, and debris flows (Melis 1997). Bankfull stage is commonly defined as the point at which flow overtops the natural channel and spreads across the floodplain. Bankfull events are relatively frequent, typical recurrence intervals of 1-2 yr for the U.S. and 1.1-1.8 yr for streams of central and southern Arizona (Moody and Odem 1999). The annual-biennial overbank flood frequency that characterizes most streams in the Southwest normally keeps riparian geomorphology and vegetation in a state of “suspended succession” (Campbell and Green 1968).

Dewatering: Drought or water table drawdown may partially or fully dewater springs eliminating aquatic and wetland function and characteristics. In many springs, natural seasonal desiccation is normal, and those springs ecosystems are characteristically depauperate in both species richness and aquatic and wetland vegetation cover. Even if relatively brief (a few hours), the first loss of permanent surface water of a previously perennial spring is undoubtedly the single largest impact of dewatering on ecological structure. While some aquatic plant and invertebrate populations may persist as propagules and recover or recolonize quickly if the spring rewaters, many are lost and the composition of the spring may be irrevocably altered. For seasonal springs that are normally dewatered, the duration and frequency of desiccation events largely controls ecosystem responses.

Sheetflow Disturbance: Depending on the dip angle of the springs, a surface sheet-flow event from heavy precipitation may constitute a significant disturbance at a springflow-dominated springs. While such storms may be rare, they may open habitat patches to colonization by long-lived plant species, and thus may be important germination events.

Rockfall: Rockfall disturbance may strongly affect the geomorphology of springs and springs microhabitats that emerge on the face, or at the base of cliffs (e.g., hanging gardens and gushets). As with flooding, rockfall may kill existing plants and rearrange microsite topography, opening sites to new colonization. Rockfall frequency is a probability distribution influenced by the integrity and composition of overlying rock, regional and micro-site climate (i.e., freeze-thaw cyclicity), and seismicity. While we suspect that the minor rockfall is relatively continuous at springs that lie at the base of large cliffs, and larger rockfalls and slope failures are rare; supporting data are not available.

Fire: Fire is little recognized as a process in springs ecology; however, springs at upper elevations on the Colorado Plateau commonly exist in heavily forested or forest meadow environments. Fire may exert profound impacts on all post-emergence characteristics and processes at springs including removal of above-ground growth, altering soil structure and nutrient spiraling, altering population dynamics, and opening terrestrial environments to colonization. Litter accumulation at springs is likely to be higher than in adjacent forests and may cause springs soils to burn more intensely than surrounding surfaces. Alternatively, increased soil moisture and profuse herbaceous ground and shrub cover may limit the intensity of burn and allow the springs to function as refugia in burned forests, protecting some species from fire and serving as population source areas for post-fire colonization of the adjacent landscapes.

Carbonate Precipitation: Carbonate precipitation is a geomorphic process that results from high $CaCO_3$ concentration in the discharging groundwater with CO_2 gas release resulting in travertine deposition. The effects of precipitation are conspicuous in Colorado Plateau streams, such as the Little Colorado River and Havasu Creek, where precipitation creates mound forms, in-channel terraces, and small to large waterfalls (e.g., Melis 1997). Geochemical precipitation effects are gradual and cumulative, but are reset by flooding. Therefore, the longer the inter-disturbance interval, the greater the impact of carbonate deposition on the spring orifice, stream and riparian microhabitats.

Interactions: Disturbance and potential productivity combine to create a gradient that strongly influences the diversity and structure of sessile organism assemblages (Table 7). Flood disturbance intensity is predicted to unimodally influence diversity. The intermediate disturbance hypothesis of Connell (1978) predicts that competition decreases diversity in low disturbance settings, disturbance reduces diversity in high disturbance settings, and disturbance also resets ecosystem developmental trajectories (Odum 1981). Huston (1979, 1994) elaborated on the intermediate disturbance hypothesis by incorporating the interacting effects of disturbance intensity and productivity on biodiversity in his dynamic equilibrium hypothesis (DEH). The DEH predicts that sessile species richness will be maximized across the disturbance intensity – potential productivity field wherever disturbance levels reach intermediate levels (Fig. 12). Such should be the case for hillslope springs vegetation and sessile invertebrates. Stevens (1989) tested this concept in unmanipulated riparian systems in Grand Canyon reporting that the hypothesis was only partially supported with more variance explained by the moisture availability (productivity) gradient. The IDH has yet to be tested at desert springs where the treatments exist most clearly. However, while productivity may produce a unimodal intermediate-peak influence on diversity (e.g., Irigoien et al. 2004), such patterns are not necessarily predictable, particularly across landscape scales (Waide et al. 1999).

Outputs: The outputs of this submodel are springs-specific microhabitat area and area changes related to the probabilities of disturbance of the various forms described. Disturbance probability is best depicted graphically using exceedance curve analysis which is a cumulative frequency curve showing the percentage of time specified flows or levels are equaled or exceeded (Vogel and Fenessey 1994). Graphical demonstration of disturbance frequency may best be assessed using the Log-Pearson Type III analysis (Appendix A). This is a statistical distribution method that has gained the most widespread acceptance and is recommended by the Texas Department of Transportation (2004) and many other flood frequency analysts. It is a statistical analysis of gauged flood data or other continuous and variable data.

These analyses require considerable monitoring data that capture small and large events. Using these outputs, disturbance frequency of all types can be applied to the TIN-GIS landscape model, and used to predict a landscape array of disturbance probability. Some forms of disturbance are linked: for example, sheetflow precipitation events may trigger flooding. Therefore, compound disturbance probabilities undoubtedly exist among some cells within the landscape. However, knowledge of the spatial dynamics of ecological resiliency may reveal how succession takes place at different kinds of springs.

Similarly, potential and actual primary productivity can be estimated across the springs landscape and the values applied to cells within the TIN landscape model. A non-technical means of estimating productivity is by clipping and harvesting living plant matter on plots of known size among the microhabitat array. Such efforts, repeated at biweekly or monthly intervals, can provide a rough estimate of how much primary production occurs throughout the growing season (Brower et al. 1990). Alternatively, CO_2 – O_2 gas analysis microcosms can be positioned throughout the landscape to measure photosynthesis rates under full sun in different microhabitats.

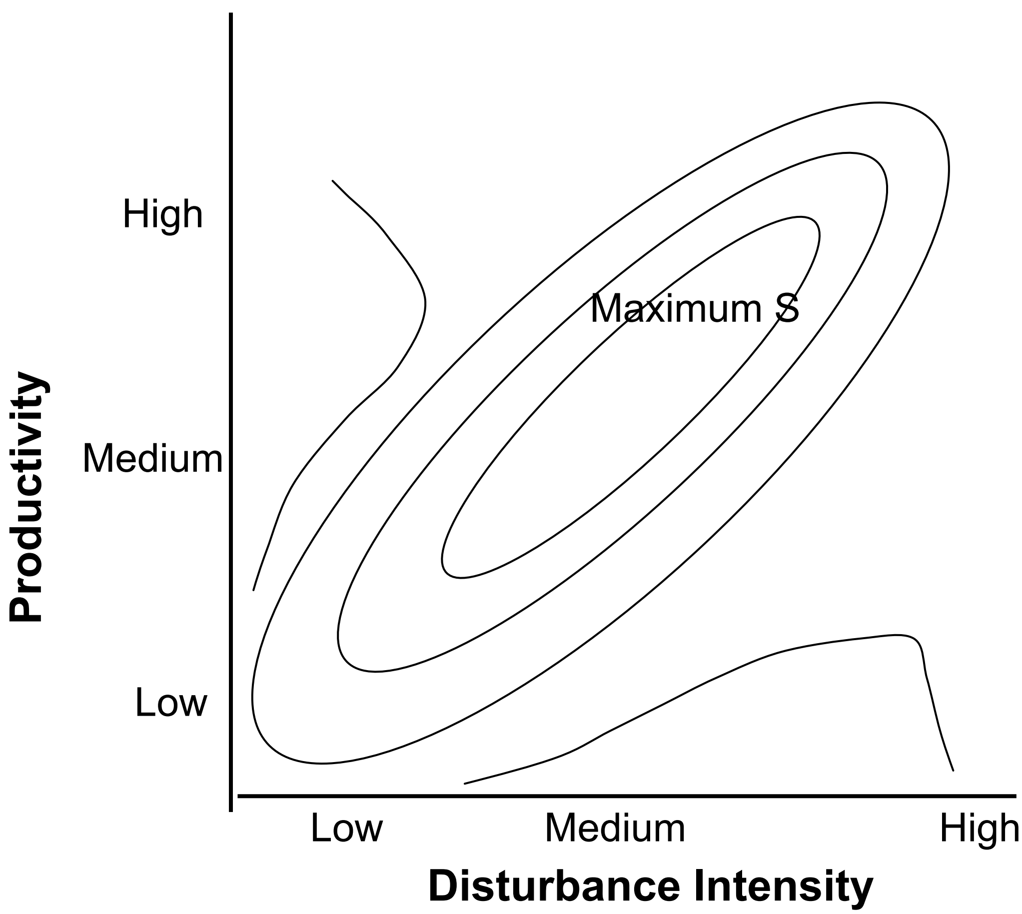


Fig. 12: Disturbance, productivity, and sessile species diversity (S; modified from Huston 1979, 1994).

Table 7: Predicted disturbance-productivity impacts on ecosystem structure and function.

DISTURBANCE INTENSITY	POTENTIAL PRODUCTIVITY					
	Low		Intermediate		High	
	Structure	Function	Structure	Function	Structure	Function
Low	Patchy ground cover of fern, moss, largely upland graminoids, and upland shrub cover; low biodiversity, but low diversity of non-native species.	Drought tolerant, long-lived assemblage, moderately competitive, low resilience, moderate levels of endemism, little habitat value.	Typically continuous ground and/or shrub cover, with some mid-canopy and tree cover; distinctive wetland and riparian vegetation mixed with upland plant species; moderate biodiversity and moderate invasibility.	Drought intolerant; moderate longevity; highly competitive, low resilience, moderate levels of endemism, good wildlife habitat value if patch size is large.	Continuous ground and/or shrub cover or strongly shaded by mid-canopy and tree cover; distinctive wetland vegetation with little upland plant elements; relatively low biodiversity and moderate invasibility.	Drought intolerant; low longevity; highly competitive, low resilience, moderate levels of endemism, excellent wildlife habitat value if patch size is large.
Intermediate	Highly patchy ground cover of fern, moss, largely upland graminoids, some upland shrub cover; moderate biodiversity, moderate diversity of non-native plant species.	Drought tolerant, moderate longevity of plant assemblage with higher annual component; moderately competitive, moderate resilience, low levels of endemism, little habitat value.	Patchy ground cover dominated by seedlings of wetland and riparian graminoids, shrubs and trees; moderate wetland-riparian-facultative shrub and tree cover; high biodiversity, moderate diversity of non-native plant species.	Drought intolerant, moderate longevity of plant assemblage with higher annual component; moderately competitive, high resilience, low levels of endemism, moderate habitat value.	Relatively continuous ground cover except immediately after disturbance events; dominated by wetland and riparian graminoids, shrubs and trees; moderate wetland-riparian shrub and tree cover; moderate biodiversity, high diversity of non-native plant species.	Drought intolerant, relatively low longevity of plant assemblage with high annual component; highly competitive, high resilience, low levels of endemism, high wildlife habitat value.

DISTURBANCE INTENSITY	POTENTIAL PRODUCTIVITY					
	Low		Intermediate		High	
	Structure	Function	Structure	Function	Structure	Function
High	Nearly devoid of ground cover, mostly consisting of upland graminoids, little shrub or tree cover; low biodiversity, moderate diversity of non-native plant species.	Drought tolerant, low longevity of plant assemblage, high annual species component; low competitive capacity, low resilience, virtually no endemism or habitat value.	Low levels of ground cover, mostly consisting of wetland graminoids, little shrub cover, but some riparian tree cover; low biodiversity, high diversity of non-native plant species.	Drought intolerant, low longevity of plant assemblage, high annual species component; low competitive capacity, low-moderate resilience, virtually no endemism, generally low wildlife habitat value.	Moderate levels of ground cover, mostly consisting of wetland graminoids, little shrub cover, but sometimes moderate riparian tree cover; moderate biodiversity, high diversity of non-native plant species.	Drought intolerant, low longevity of plant assemblage, high annual species component; moderate competitive capacity, moderate resilience, virtually no endemism, generally moderate wildlife habitat value.

Ecosystem Consequences: Rapid geomorphic alteration may arise at springs in disturbance- prone settings. The role of the basin climate in determining aquifer dynamics has been described above (Submodel 1, Table 3), and climate also affects storm event frequency and the likelihood of flood-related disturbance of in-channel springs and those subject to inundation, fire, or rockfall. Springs that emerge on the floor of flood-scoured stream channels are likely to have highly dynamic vegetation and invertebrate faunae. Flooding affects sediment transport, channel geometry, instream depth-velocity-substratum relations and microhabitat development, riparian terrace structure and composition, and soil development. This is particularly apparent in natural bedrock-dominated settings, such as in Grand Canyon, where little riparian vegetation develops. Ten-year return frequency floods are approximately 12.5-fold larger, and 100-yr events are approximately 25-fold greater, than the mean pre-dam baseflow of the Colorado River at Lees Ferry (Stevens et al. 1995). The 10-yr flood events were sufficient to prevent perennial vegetation from existing in the flood-scoured Colorado River corridor (Webb 1996).

Variation in the magnitude, duration, frequency, and timing of flow, dewatering, and rockfall disturbance events creates a disturbance intensity regime that strongly affects biological assemblages (Table 7; Fig. 13). However, few studies of springs productivity or relation to the disturbance regime have been published. Perla and Stevens (2002) examined a relatively natural spring in Grand Staircase-Escalante National Monument in southern Utah, reporting that productivity levels were 1-2 orders of magnitude greater at the spring than in wet grazed and dry grazed riparian habitats and 1-2 orders of magnitude greater than in the surrounding grazed, arid uplands. They reported that vegetation structure was significantly different as well, with relatively little wetland ground cover, much willow (*Salix* sp.) shrub cover, and considerable middle and upper canopy cover.

The interaction between flood disturbance intensity and potential productivity has been tested and supported by Resh et al. (1989) in aquatic systems, and by Stevens (1989) and Pollock et al. (1998) in riparian systems. Further consideration should be given to the productivity-related factors that collectively create springs and riparian “fertility gradient” (*sensu* Day et al. 1988), including primary productivity, decomposition, and nutrient cycling. Pollock et al. (1998) tested the DEH along an Alaskan river floodplain using detailed measurements of flood disturbance and productivity, as described above. They reported variation in both disturbance intensity and potential productivity across a river floodplain, and found support for the DEH. This study is one of the few to approach variation in these ecological factors on a landscape basis at a spatial scale relevant to plant populations; however, riparian vegetation systems are not ideal for studying the DEH because disturbance and productivity gradients are parallel: high disturbance = high productivity. No low disturbance – high productivity treatment combinations occur naturally in fluvial riparian systems. The DEH remains to be tested in desert hillslope springs ecosystems, where all treatment combinations of low, intermediate, high disturbance and productivity exist.

This submodel indicates that natural disturbance intensity and potential productivity vary considerably at different kinds of springs. Depending on site configuration, springs-flow dominated springs, such as hillslope springs, may be low disturbance sites with strong paleorefugial function (Fig. 12). Such springs are likely to support endemic species and, depending on their size and type, may host high biodiversity of relatively rare species. In contrast, stream-flow dominated springs (e.g., in-channel springs) are usually highly disturbed by flooding and are more likely to support weedy species (perhaps at high levels of species density) with few endemic species and rapid floral and faunal turnover. These geomorphic constraints may be strongly moderated by microclimate and productivity. Thus the geomorphic disturbance and potential productivity context of a springs play important roles in its ecological and evolutionary role as an ecosystem.

<u>Habitats Template Submodel 5</u>

Springs ecosystems exist as complex mosaics of microhabitats, particularly in topographically diverse terrain. As many as 13 distinct microhabitats may exist at the 11 common subaerial springs types found on the Colorado Plateau (Table 2). Springs types vary in their microhabitat diversity as follows:

Gushet > Hanging garden = Rheocrene > Fountain >
Limnocrene = Hillslope = Mound-form = Geyser >
Helocrene = Cave > Hypocrene

The size of the springs greatly influences the number of microhabitats created, but overall, hanging gardens, gushets and rheocrene springs tend to have the greatest microhabitat diversity.

Microhabitats arise from the geomorphic and microclimate properties and processes described in submodels 1-4 and constitute the template on which springs biological assemblage develop (Fig. 13). These microhabitats are important because each may support relatively discrete assemblages, and interactions of species among microhabitats are likely to vary as a function of habitat connectivity and species autecology.

The 13 common springs microhabitats encountered at Colorado Plateau springs do not occur equally. From Table 2, the frequency of occurrence of microhabitats across all springs types is:

Adjacent uplands > Adjacent dry rock >
Riparian = Spring stream = Pools = Orifice >
Low-slope wet meadows > Wet wall > Madicolous =
Hyporheic > Hillslope meadow > Spray zone = Cave

While some microhabitats occur in relatively low frequency, the numerical abundance and area of those microhabitats may be greater than other, more frequently encountered microhabitat types. This is because the springs types with which they are associated may be more common. For example, hanging gardens are a relatively common type of springs on the Colorado Plateau and typically have wet backwalls and plunge pool microhabitats, which occur moderately to relatively infrequently at other springs types.

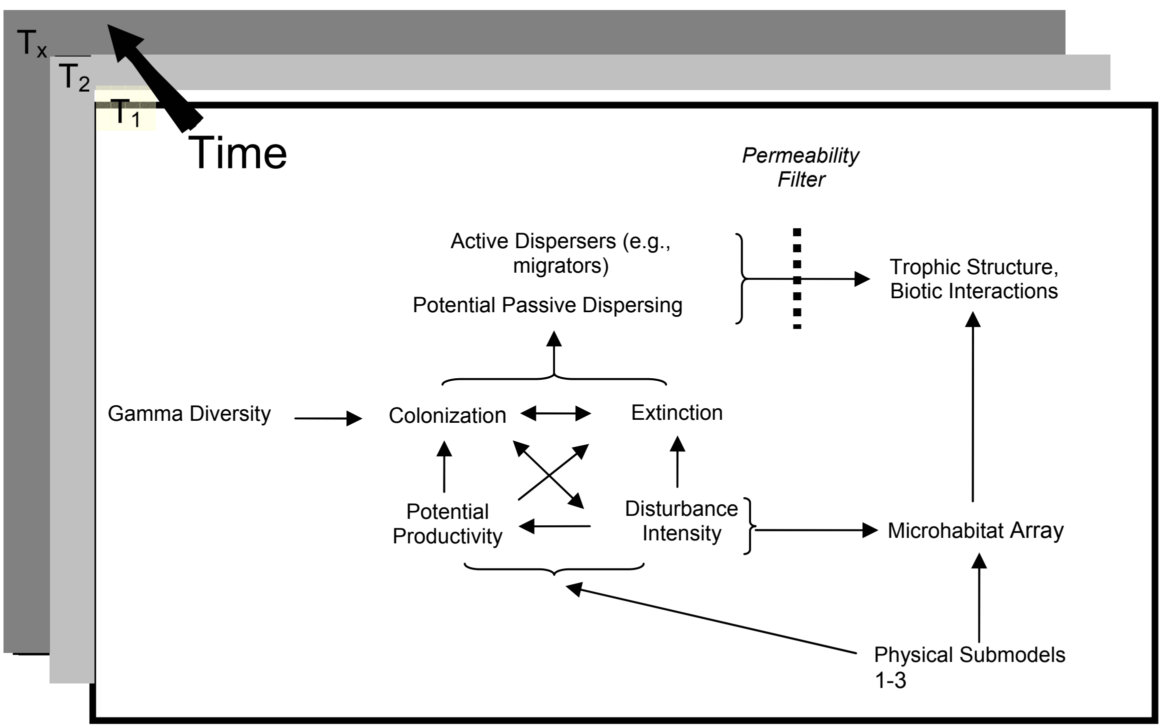


Fig. 13: Relationships between Biogeography Submodel 6 components and physical Submodels 1-3, habitat-related Submodels 4-5, and ecosystem trophic structure Submodel 7. T_1-T_X is the ecosystem condition at time 1 through future time x.

<u>Biogeography Submodel 6</u>

Overview: The biogeography submodel describes the composition of springs assemblages that develop on the microhabitat template of Submodel 5 over time under the physical constraints of Submodels 1-4 (Figs. 2, 13, 14). It consists of two components. Submodel 6a is based on the concept that the arrival of potential springs colonists (via various dispersal mechanisms) is governed by an island biogeographical colonization-extirpation process with constraints imposed by the size and isolation of the springs. In Submodel 6b, further, local constraints are imposed by both the springs microhabitat quality and the biological permeability of the existing ecosystem

The pool of potential colonists includes sessile, passively-dispersing taxa (e.g., many plants), and actively dispersing faunae (e.g., birds; Bullock et al. 2002). Potential colonists encounter established assemblages that have varying levels of permeability depending on biogeographic processes, disturbance processes, as well as assemblage history (Fukami and Morin 2003). Collectively, these processes shape the instantaneous composition and population dynamics among the various springs microhabitats (Submodel 5) and this dynamic assemblage structure interacts trophically (as described in Submodel 7, below).

Biogeographical Drivers – The Regional Species Pool: The local assemblage of species (ß-diversity) at a springs is a subset of the diverse regional pool of species (γ-diversity) that may disperse through “jump” (rapid long-distance), “diffusion” (slow outward range expansion), and “secular” (evolutionary range expansion) mechanisms (*sensu* Brown and Lomolino 1998; Bullock 2002). “Assembly rules” may apply to the arrival schedules of these potential colonists: passively dispersing species may arrive in a temporally ordered fashion with weedy, eurytolerant taxa arriving first, and less vagile, more stenotolerant, and sometimes more competitive taxa arriving later (Diamond 1975, but see Gotelli and Graves 1996). The developmental history of the assemblage may alter the permeability of the ecosystem to new colonists (Fukami and Morin 2003).

Passive dispersal mechanisms typically involve transport by wind, water, or gravity. The orientation of springs in the landscape with respect to dominant anisotropic winds may affect the arrival schedule of liverworts, mosses, lichens, ferns, and other taxa as has been demonstrated in Southern Hemisphere islands (Muñoz et al. 2004). If the runout streams of a suite of springs are connected in a stream basin, flow-related transport of species from upstream springs may eventually result in colonization of downstream springs. Rockfall or simple gravity fall is likely to result in downslope transport of propagules with establishment at least partially influenced by habitat quality at lower elevations (smaller elevation jumps are more likely to be successful, as high elevation species are likely intolerant of low elevation climates). This process may partially account for higher species richness of wetland plants at intermediate elevations in the Grand Canyon region (Fig. 9).

Actively dispersing species include strong-flying invertebrates, birds, bats, and some larger mammals, and the hitch-hiking fauna they transport. These species may search out and preferentially use springs as stop-over, foraging, or breeding habitats. For example, north-migrating southwestern birds are opportunistic, preferentially searching out patches of riparian vegetation as stop-over habitat (Skagen et al. 1998). Springs are heavily used by breeding birds as well: Grand Canyon Wildlands Council (2002) reported 35 breeding bird species (some in great abundance) in less than an hour arriving to water and feed at Cliff Springs on the North Rim of Grand Canyon. This high level of avian use was attributed to the isolated location of the springs as a water source.

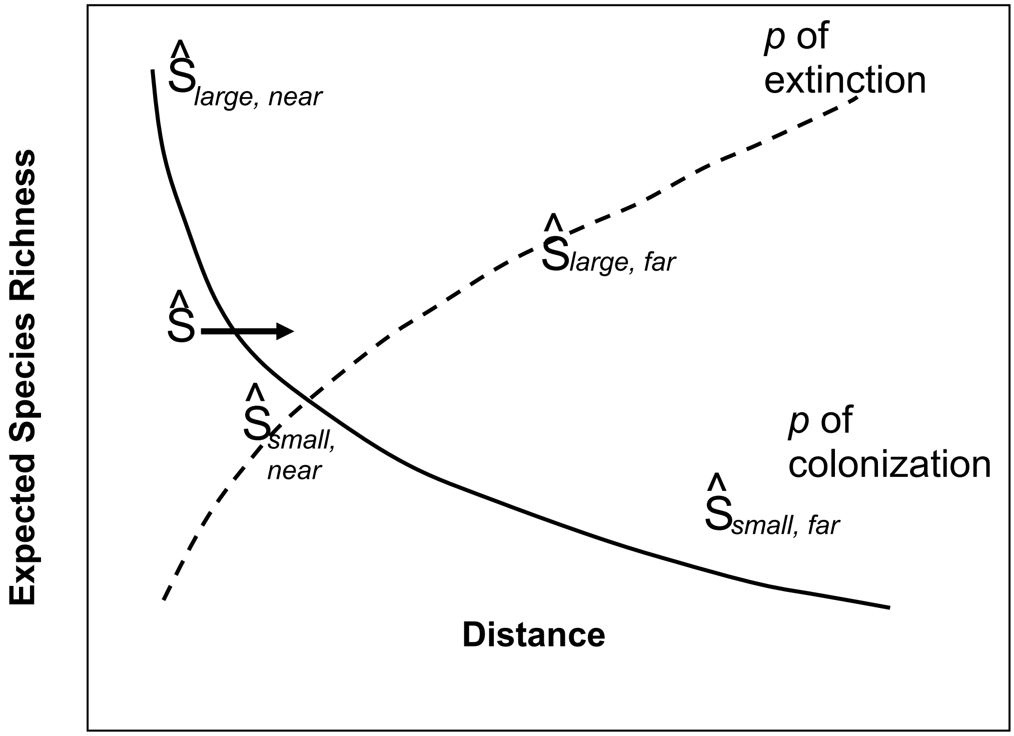


Figure 14: Island biogeography submodel (MacArthur and Wilson 1965). $_i$ is the expected number of sessile, passively dispersing species (e.g., plants) at an individual springs ecosystem *i*, given its size and distance from other springs. Other values are for springs of varying size and distances. The two lines are probabilities of colonization and extinction over distance from other springs.

Colonization-Extirpation Dynamics: Colonization and extirpation probabilities form the core interaction determining species-area relationships in island biogeography theory (IBT; MacArthur and Wilson 1965, Wardle et al. 2003). IBT posits that the biodiversity of passively dispersing species should be related to the size and isolation of habitat patches (in this case springs ecosystems; MacArthur and Wilson 1965; Fig. 14). Larger islands near other islands are more likely to have higher species richness as a result of higher colonization probabilities and lower extirpation probabilities, as compared to smaller, isolated springs. Grand Canyon Wildlands Council (2004) provided evidence supporting this pattern using springs on the Tonto Platform of Grand Canyon (Fig. 15). Increased probability of both colonization and extirpation over time are offset by successional development of the habitat patch (Fig. 15).

The IBT also does not well predict the diversity of actively dispersing species which may strongly affect local springs and streams ecosystems. For example, desert bighorn sheep (*Ovis canadensis nelsoni*) selectively browse all *Lobelia cardinalis* flowers at several Grand Canyon springs (Stevens, personal observation) and this mammalian herbivory may prevent seed production in this desert springs specialist plant. Other mobile species may congregate and take advantage of novel resources. For example, Brown et al. (1989) reported the discovery and exploitation of abundant spawning rainbow trout (*Onchorhynchus mykiss*) by migratory bald eagles (*Haliaeetus leucocephalus*) at spring-fed tributaries of the Colorado River in Grand Canyon. Such predation may shift the developmental trajectory of the affected assemblage, particularly if the predators “remember” the locality and repeatedly return to exploit it (apparently the case among bald eagles).

The IBT does not necessarily account for organism abundance within islands (Wardle et al. 2003), as island size may promote abundance of some species but reduce those of others. Time since disturbance, water chemistry, microsite geomorphology, dip angle (rockfall disturbance intensity), slope aspect, and other site factors are likely to play strong roles in determining the population fate of populations, roles that may be relatively independent of the colonization-extinction species richness. This decoupling of diversity and population dynamics is partially responsible for the general observation that each springs ecosystem is unique with a particular assemblage and distribution of species (Grand Canyon Wildlands Council 2002).

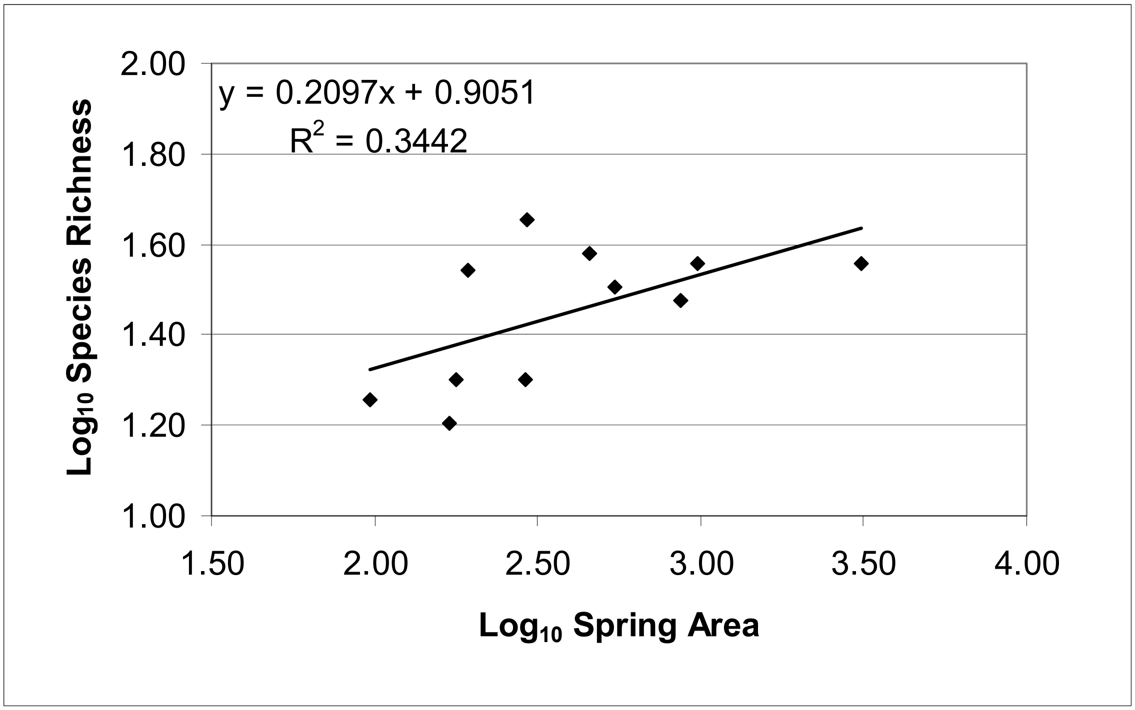


Fig. 15: Species-area relationship for higher plants at middle elevation springs in Grand Canyon, Arizona (Grand Canyon Wildlands Council 2003).

Interactions (Submodel 6): IBT influences on springs diversity are moderated by interactions between the physical disturbance and productivity gradients within microhabitats over time, shaping the composition and structure of the assemblage in the various microhabitats (Fig. 16), and their permeability (Fig. 13). Aquatic and wetland vegetation are likely to respond rapidly to major changes in flow, whereas riparian vegetation and the colonization of upland plant species are likely to respond more slowly to such changes. The ecological trajectory of assemblage compositional changes is not necessarily predictable (successional), particularly if multiple physical or anthropogenic impacts occur simultaneously. For example, as springs ecosystems become increasingly more isolated and fragmented, colonization is likely to be reduced and extirpation is likely to be exacerbated. These interactions may result in a gradual reduction in species richness at springs over time (Fig. 16).

The biological permeability of a springs ecosystem to new colonists varies in response to competition and predation interactions, successional stage, and assemblage composition of previously established individuals (Fig. 13). Fukami and Morin (2003) used laboratory tests on microbial assemblages to demonstrate that the history of community assembly (e.g., from random first arrivals of species from the γ-diversity pool) may greatly affect subsequent assemblage structure. They reported that the productivity-diversity structure of microbial assemblages took different forms 30 generations after initial colonization under five productivity regimes. In some cases the relationship was unimodal, but in other cases it was non-significant. At Colorado Plateau springs, the arrival and establishment of cottonwood (*Populus* spp.) trees may greatly alter habitat characteristics (i.e., shade, litter accumulation, avian assemblages).

Submodel Structure and Outputs: The biogeography submodels include estimates of passively and actively dispersing species γ-diversity and ß-diversity with an inventory and GIS-based description of the physical setting and characteristics of individual springs, their sizes and nearest-neighbor isolation metrics, as well as a synthesis of information on regional frequency of occurrence of springs species and an index of assemblage permeability by new colonists (Fig. 13). With these inputs, analysis of the submodel will involve a multivariate principal components-style analysis of numerous springs in the region. This species-environment analysis describes relationships among species and functional groups in relation to IBT and springs physical habitat modifiers. Such analyses provide biplots of principal component loading scores for species as well as an interpretation of the importance of the various biogeographic and physical factors affecting springs biodiversity.

The Submodel 6b index of permeability value for plants (as passive dispersers) may be derived through a demographic analysis of seedling establishment frequency among various wetland plant taxa, modified by an index of successional stage. The number of seedling new species which are not part of the present or recent assemblage is calculated in relation to the total number of wetland and riparian plant species in each microhabitat. This number is likely to be zero or low. Successional stage is estimated as the duration in years since the microsite last sustained a major disturbance. Alternatively the amount of open, unvegetated but suitable germination habitat may provide an alternative adjustment of this index. On long-term study plots, experimental opening of habitat patches may be used to test and refine this index.

Implications: The biogeography Submodel 6a factor loading scores may be analyzed statistically and used to interpret habitat associations and functional group traits (i.e., for active dispersers) in relation to environmental variables. Such analyses are common in the ecological literature (e.g., Stevens et al. 1995, 1997b), Wimp and Whitham (2001) and are useful as descriptions and for developing testable hypotheses about observed relationships among variables; however, they are not useful as predictive models.

Coupling the disturbance-productivity elements of Submodel 4 with the habitat templates Submodel 5 and the biogeography submodel 6 yields complex, but predictable consequences for springs ecosystem processes and assemblage characteristics (Fig. 17). A given springs assemblage will be partially structured by the combination of species responses to disturbance and productivity, IBT colonization-extinction dynamics, and the duration of assemblage development.

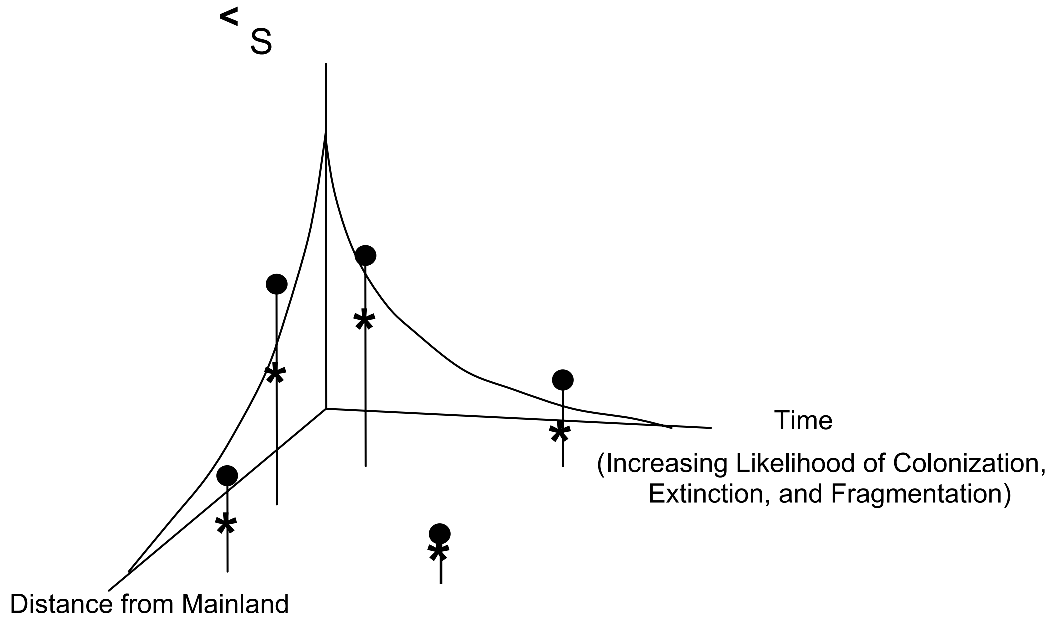
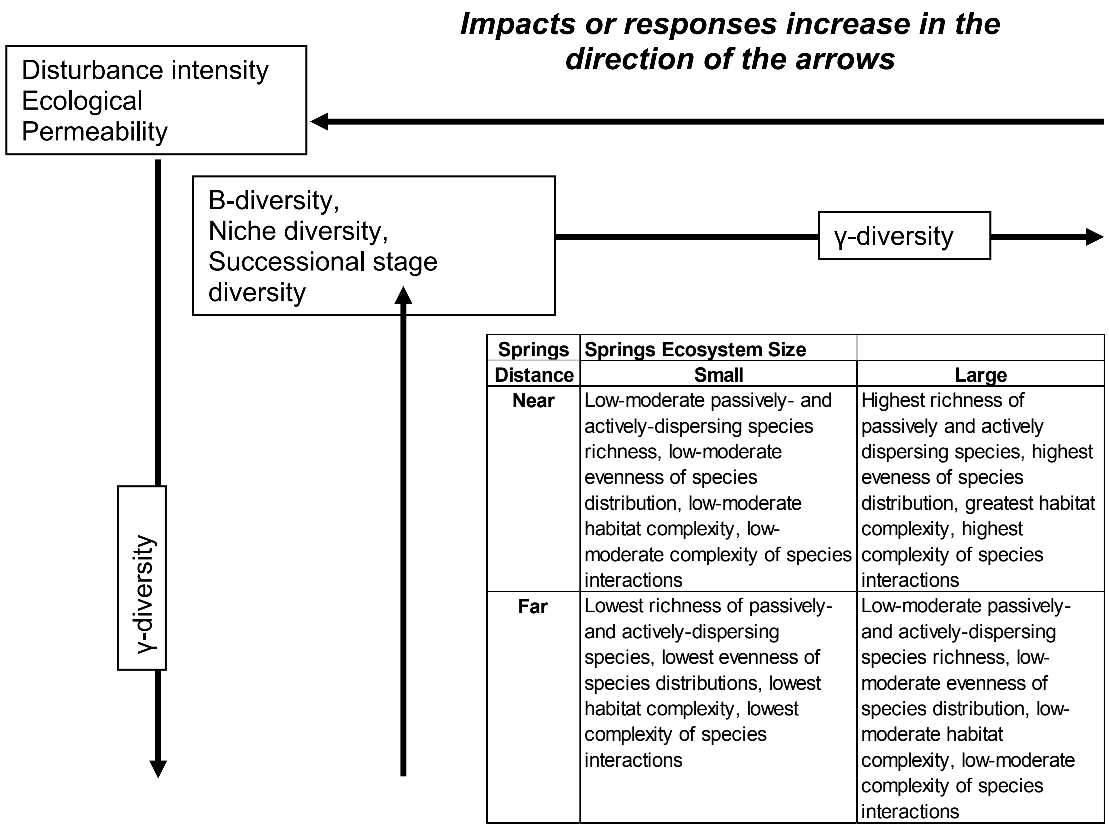


Figure 16: Temporal (successional) effects of habitat fragmentation on expected springs plant species richness (S). Filled dots are for large islands or habitat patches at varying distances from source pools, and asterisks are small habitat patches.



Springs Distance	Springs Ecosystem Size: Small	Springs Ecosystem Size: Large
Near	Low-moderate passively- and actively-dispersing species richness, low-moderate evenness of species distribution, low-moderate habitat complexity, low-moderate complexity of species interactions	Highest richness of passively and actively dispersing species, highest eveness of species distribution, greatest habitat complexity, highest complexity of species interactions
Far	Lowest richness of passively- and actively-dispersing species, lowest evenness of species distributions, lowest habitat complexity, lowest complexity of species interactions	Low-moderate passively- and actively-dispersing species richness, low-moderate evenness of species distribution, low-moderate habitat complexity, low-moderate complexity of species interactions

Fig. 17: Colonization-extirpation (IBT) and biogeography modifier impacts on springs diversity, ecosystem structure and function.

Assemblage-Trophic Dynamics Submodel 7

Overview: Depending on physical setting, disturbance, and biogeographic process impacts on assemblage development, springs ecosystems may develop weak or strong trophic structures with feedbacks to constituent habitats through decomposition and nutrient spiraling (Elwood et al. 1983; Fig. 2). The trophic submodel describes the populations, composition, standing mass, foodweb structure and dynamics, and temporal change of the assemblages that develop on the several to many microhabitats within a springs ecosystem (Fig. 18). The model consists of two parts that may be applied to each microhabitat or to the springs as a whole: a) a population composition and dynamics submodel that provides both a means of modeling individual populations based on life history and habitat data and also results in a description of the species richness, diversity, species density, and resulting habitat structure (i.e., plant cover by stratum); and b) trophic structure and interactions with instantaneous-annual standing mass, productivity, ecological efficiency, and resiliency. Temporal changes (successional) are expected throughout these states and processes, and these components are modified by the previous six physical and biogeographic submodels. The outputs of Submodel 7 are ecosystem goods and services, including some variables that may be useful for monitoring ecosystem integrity. We note that aquatic-terrestrial linkage appears to be far stronger in streamflow-dominated springs than in stream ecosystems.

7a Drivers: Springs ecosystem assemblage composition and structure is described through general, instantaneous-annual measurements of species richness, diversity, species density, and habitat structure (i.e., plant cover by stratum; Fig. 18). These variables arise through physical and biogeographic interactions and constitute much of what is normally ascribed as springs ecosystem structure. The

Submodel 7a population dynamics component is designed to address the population dynamics of a sensitive (endangered or endemic) species of plant or animal, often a concern for springs managers. Population dynamics modeling for a species that exists throughout its lifespan in specific springs microhabitats are typically based on life history table analyses in the context of microhabitat area relationships (Hannon and Ruth 1994). The density and reproductive potential and potential mortality of individuals at various points in the life history can be related to its habitat area and quality and used to model potential population size and determine critical periods for a population. These models require basic demographic and life history traits, but can effectively simulate the progress of a population through periods of stress such as may be caused by human alteration of springs. Such models involve accounting for age-specific survivorship, differential mortality, and expected reproductive output at different life stages. Cohorts are modeled as they "move" through the model and ecosystem changes in composition, physical and biological structure, and composition can be monitored over time.

Two examples of springs species' population models have been developed for endangered species in Grand Canyon. Three years of intensive population analyses and microhabitat surveys at Vaseys Paradise spring revealed that the endangered Kanab ambersnail (Succineidae: *Oxyloma haydeni kanabensis*) population reached its lowest levels of density during spring; and that winter survivorship was, in part, related to the irregular timing of non-native watercress (*Nasturtium officinale*) development, the host plant species on which the snail developed to reproductive size most quickly (Stevens et al. 1997a, Spamer and Bogan 1997-1998, Sorensen 2001). Interestingly, these studies indicate that this endangered land snail population has increased as a result of flood control by Glen Canyon Dam as well as expansion of non-native water-cress into its habitat.

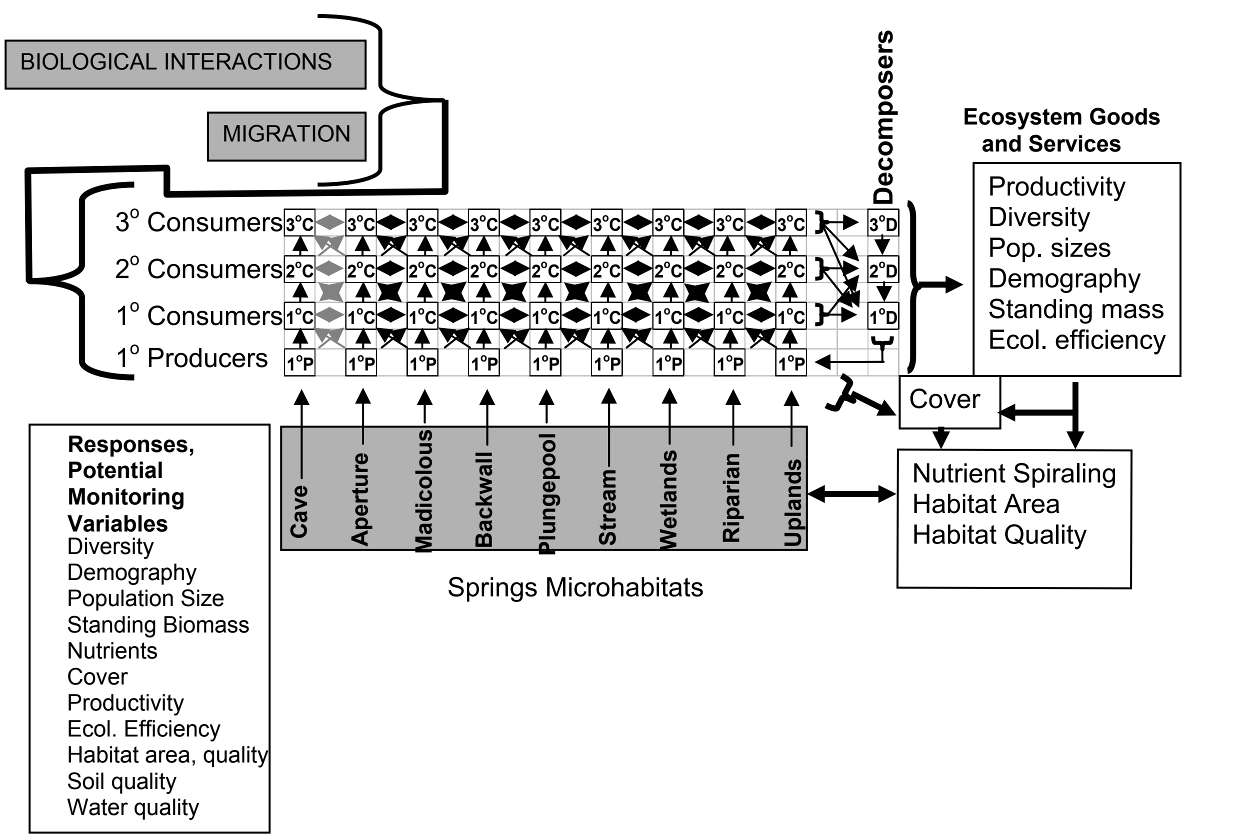


Fig. 18: Instantaneous assemblage composition, structure, and trophic interactions Submodel 7, and ecosystem goods and services Submodel 8.

Population modeling of species that are not obligatorily restricted to springs are far more challenging because of multiple sources of mortality, unstudied fate in the different environments inhabited, and multiple weak impacts of other physical and biotic factors. The case of the endangered humpback chub (HBC) is most informative. HBC commonly live in the Colorado River in Grand Canyon and only spawn successfully in the springfed lower Little Colorado River. While it is clear that the distribution of this species has been reduced following closure of Glen Canyon Dam upstream, at least seven hypotheses have been suggested that may account for the (declining?) status of this species: 1) the impacts of constantly cold mainstream water temperatures, particularly on young fish emerging from the Little Colorado River; 2) predation by nonnative trout and other predatory fish, 3) competition by non-native fish, 4) scientific handling intensity, 5) habitat limitation in the mainstream, particularly loss of backwater nursery microhabitat, 6) parasitism by nonnative *Lernia* copepods and Asian tapeworms , and 7) dam-related loss of floods that may cue major spawning runs.

Population modeling of humpback chub is complicated by the inability to detect spawning activity in the only remaining spawning habitat, its movement among the mainstream Colorado and Little Colorado rivers, and the substantial uncertainties in recruitment in the fish population model. It should be noted that more than $100 million has been expended on determining the status and trends of HBC, and success in that effort is not apparent. Therefore, modeling of complicated life histories of organisms that inhabit multiple environments, including springs, may not prove effective or affordable. However, this component of the overall trophic model cannot be expected to describe complex interactions among multiple species. This population submodeling component is introduced because of the often species-specific population information needs faced by federal and state managers, but it is not necessarily critical for the general ecosystem trophic dynamics in Submodel 7b.

7b Drivers: Foodweb associations are generally determined through a combination of observation, dietary analyses, and stable isotope research. Such ecosystem energetics were first described by Lindeman (1942) in Cedar Bog Lake and Lake Mendota. Subsequently, Odum (1957) related ecosystem energetics to the processes of succession and refined those metrics at Silver Springs, Florida. The energetics framework provides a convenient means to integrate physico-environmental state variables and processes to habitat availability, biogeography, trophic structure and interactions, productivity, decomposition, and composition in the overall ecosystem. This approach has potential for distinguishing trophic levels and ecological roles (e.g., predation) while integrating springs ecosystem structure, development, function, and response to natural and anthropogenic disturbances through a common metric. If coupled with landscape modeling of habitat patch dynamics, this approach may contribute substantially to springs ecosystem theory and site-specific predictions about springs responses to disturbances. The trophic perspective provides a suitable framework for conceptual modeling as it quantifies interactions between state variables, physical processes, and natural and anthropogenic stressors in relation to springs response variables (e.g., vegetation cover, biodiversity, population variables) that are most likely to be important for monitoring, management and springs restoration.

Model Structure and Outputs: The assemblage trophic structure model consists of description of the assemblage composition, diversity, structure, and other factors. A food-web diagram is useful for identifying trophic linkages, and an energetics analysis is useful for integrating these elements into an empirical ecosystem energetics model. Such a model emphasizes instantaneous standing mass, productivity, ecological efficiency, and resiliency, processes and features that naturally change over short- to long time frames (Fig. 18).

Time is a transitionally independent variable in these analyses with effects vectored through various physical and ecological developments. Temporal changes in ecosystem composition, structure, and function occur in response to disturbances, developmental duration, and seasonality. These changes may be predictable (successional) or not, and may vary within microhabitats or across entire springs. In general, we subscribe to the ecosystem developmental trajectory concept of Odum (1981), in which assortative processes first increase then slightly decrease species richness and ecosystem respirational energy loss. Such changes are associated with tight (springsflow-dominated) or low-moderate (surface-flow-dominated) nutrient and other materials cycling that may occur in springs. Although present data are inadequate to accomplish a full trophic analysis of any springs ecosystem, the model here has the potential to provide a landscape-based ecosystem energetics analysis of important ecosystem goods and services that may be tracked through time and anthropogenic environmental alteration.

Implications: In addition to general ecosystem characteristics, such as diversity, percent cover of different plant species and strata, and individual population models, assemblage trophic Submodel 7 predicts a given springs' community productivity, respiration, and ecological efficiency. Collectively, these generate springs ecosystem characteristics, flow, and biological products, which are the ecosystem goods and services of Submodel 8. Although present data are inadequate to accomplish a full trophic analysis of any springs system, the model here has the potential to provide a landscape-based ecosystem energetics analysis of important ecosystem goods and services that may be tracked through time and anthropogenic environmental alteration. Our concluding Submodel 8 identifies the outcomes of this model more completely.

Ecosystem Goods and Services Submodel 8

The controls model describes the output of goods, services, and feedbacks provided by springs ecosystems to the ecosystem and to humans (Figs. 2, 18). Exploitable resources include water, wood, arable land, wildlife, and recreational values, as well as services (e.g., providing water for human or livestock consumption or irrigation). These aquatic and riparian goods and services and linkages are dependent on the natural functioning of the previous seven submodels and are subject to change both in response to natural processes and anthropogenic stressors (see below). This component of the controls model describes the collective output from the previous models, which are viewed as being important to ecosystem function, characteristics, and/or human value or use. Some ecosystem products, such as organic production and vegetation development, strongly feed back into habitat area and quality (i.e., pedogenesis, microclimate, nutrient spiraling, etc.), enhancing future ecosystem integrity. Many of the characteristics of springs, such as flow or increased shading from tree cover, provide essential feedback into assemblage composition and structure. Trophic dynamics result in primary and secondary production that feed higher trophic levels, sometimes including humans.

In addition to traditional goods and services, some of the outputs of the Controls Model represented by Submodel 8 are variables that are likely to be useful for monitoring including diversity, demography, population size, standing biomass, nutrient concentrations, cover, productivity, ecological efficiency, habitat area and quality, soil quality, flow quantity and variability, and water quality. Monitoring some or many of these variables may help managers understand how springs function and change in response to human stressors (below).

Anthropogenic Stressors Model

Although reverence for water miraculously emerging from the earth runs deep and widely professed, it has done little to protect springs ecosystems from the onslaught of human exploitation. Springs have a lengthy history of poor management, and many have been so thoroughly altered by humans that ecological restoration often must be based on guesswork or regional modeling. Springs are manageably small, highly diverse and productive ecosystems. Care for the aquifers that feed them and a modicum of conservation attention and foresight to springs can result in substantial protection of regional biodiversity and ecological integrity. Because of the biological importance, threatened status and potential resilience of springs ecosystems, the improvement of understanding, protection and restoration should be high priorities for land management and conservation agencies.

In this section, we review existing documentation of anthropogenic impacts on Colorado Plateau springs and discuss several common types of springs stressors. We then describe the overall anthropogenic state-and-transition stressors model, describing the impacts of multiple stressors on each of the controls submodels. We then describe how specific kinds of human impacts affect springs indicator variables. Lastly, we develop and test a means of measuring stressor impacts on different ecosystems and microhabitats. Overall, this stressors model may help springs managers identify variables of interest, monitoring frameworks, and triggering criteria for actions.

Human Impacts on Colorado Plateau Springs

Overview: Human activities have greatly reduced the ecological integrity of many wetland, riparian and springs ecosystems through competing exploitative uses, including groundwater depletion, fuel wood harvest, recreation, livestock grazing, and wildlife management (Thomas et al. 1979, Johnson et al. 1985, Gregory et al. 1991, Mitsch and Gosselink 1993, Glennon 2002). Overall estimates of riparian habitat loss range from 40%-90% among the southwestern states (Dahl 1990), but assessment of human impacts at springs is only now emerging.

The array of specific anthropogenic stressors at springs was documented at >220 springs in northern Arizona on the southern Colorado Plateau (Grand Canyon Wildlands Council 2002, 2004; Stevens and Springer, unpublished data). Springs were categorized on the basis of their observed ecological integrity as being in poor (obvious, severe, and ecologically debilitating impacts), moderate (having flow, having conspicuous human impacts, including dominance by non-native species but still having some ecological function), and good (having substantial ecological function and not being dominated by non-native species) condition. These data demonstrate that more than 93% of springs on federal, non-National Park Service lands have been ecologically devastated or are functioning at risk. Even springs within highly protected management units, such as Grand Canyon National Park, have a lengthy history of anthropogenic use and alteration (Grand Canyon Wildlands Council 2002). In another study, Long et al. (in press) documented wildfire impacts at moderate and high elevation springs on the White Mountain Apache Indian reservation. Flood and fire-induced site erosion impacts at <20 percent of more than 55 springs and other natural water sources, but the affected sites were seriously altered. They concluded that appropriate management both before and after wildfires reduced losses of springs habitats and ecosystem function. Collectively, these studies indicate that humans affect virtually every physical and biological ecosystem springs process, component and characteristic including climate, aquifer dynamics, groundwater quality, regional habitat fragmentation and local disturbances, introduction of non-native species, hunting, grazing, mining, direct visitation or adjacent construction impacts on ecosystem integrity.

Specific Anthropogenic Stressors and Consequences

Altered Regional Groundwater Availability: Alteration of springs flows may arise from several potential anthropogenic impacts (Glennon 2002) on aquifers. Anthropogenic climate change may reduce precipitation, infiltration and aquifer dynamics. Land-use change may alter the processes for recharge to an aquifer. For example, urbanization leads to an increase in impervious surface area over an aquifer, increasing the amount of surface runoff and decreasing the potential for recharge. Also, changes in land use by fire suppression or grazing can change the role of plant water use in a watershed and subsequently recharge to the aquifer. Reduction of the water-table elevation or well-drilling may allow inflow of lower-quality groundwater into an aquifer. In addition, pollution of percolating surface water or groundwater may reduce the quality of an aquifer's water. Extraction of groundwater from the aquifer may partially or wholly dewater individual springs or entire complexes of springs resulting in fragmentation of habitat, increasing isolation of springs ecosystems, and interruption of biogeographic processes at microsite-regional spatial scales in perpetuity.

Groundwater augmentation may occur when aquifers are artificially recharged by urban run-off, when reservoirs increase water tables, or through climate changes that increase precipitation. Increased springs flow is often accompanied by a change in flow chemistry and pollutants.

Pollution: Groundwater and surface water pollution strongly alters springs ecosystem integrity and is a common phenomenon in agricultural and urban areas. Agricultural groundwater pollution may shift ecosystem nutrient dynamics to entirely novel trajectories creating conditions to which few native species may be able to adapt. Non-point-source agricultural fertilizers have contaminated virtually all of the springs in Florida which emanate from shallow aquifers (T. Scott, personal communication). Such increases in pollutant concentrations constitute a "push" form of disturbance on springs with effects lasting at least for more than the duration of the recharge cycle.

Local contamination may also affect springs microhabitats by polluting surface waters. Such impacts are abundant at springs on the southern Colorado Plateau where springs sources are often fenced and concentrate ungulate use (Grand Canyon Wildlands Council 2002).

Local Flow Diversion: Springs have long been the target of human alteration to improve water supplies for culinary, livestock, and other uses. Following the lead of the Environmental Protection Agency, most states require that groundwater used for culinary purposes remain below-ground thereby avoiding exposure to surface contamination. The implications of this legal requirement have commonly meant that springs sources are dewatered before point of emergence or that facilities are constructed over the springs (spring boxes, spring houses, etc.), voiding their ecological functions.

Grand Canyon Wildlands Council (2002) noted several forms of springs flow alteration including diversion from the pre-orifice (prior to the point of emergence) or post-orifice (after emergence) environment. Pre-orifice diversion is often achieved by: 1) sealing the springs orifice from bedrock (and sometimes sealing the surrounding bedrock fractures) and installing piping; or 2) excavating the springs source in colluvium or alluvium, installing a slotted pipe catchment system, back-filling the excavation, and piping the water. Grand Canyon Wildlands Council (2002) noted that diverted springs flows on the Arizona Strip were sometimes piped more than 30 km from the source to the delivery point.

Post-orifice diversion is also common, particularly for livestock watering and development of ponds. Spring flows are commonly captured into open troughs or into covered tanks and then piped to troughs or ponds. These alterations may preserve some ecological function at the springs source, but often eliminate spring channel and cienega (wet meadow) functions.

Interruption of Disturbance Regimes: Humans commonly influence the frequency and type of disturbance, impacts that strongly affect springs ecological development. Surface-flow dominated springs are characterized by frequent flood events and considerable interannual flux in vegetation cover and diversity. For example, Grand Canyon Wildlands Council (2004) detected 10-70 percent variation in vegetation cover in one such springs that was monitored for three years. Moderate to high variability in the size and spatial arrangement of vegetation patches or aquatic invertebrate composition in such settings is a normal system attribute, and resilience to disturbance may be the only useable metric of ecosystem health other than wetted area or flow. Flow regulation may stabilize normally highly disturbed streamside springs ecosystems altering structural, functional, and trophic characteristics of springs. For example, Stevens et al. (1997a) reported that flood control of the Colorado River in Grand Canyon by Glen Canyon Dam resulted in a 40 percent increase in vegetation cover of Vaseys Paradise spring. This increase in habitat area likely allowed a large expansion of the endangered Kanab ambersnail population there. Flow regulation of ephemeral stream channels on the Colorado Plateau commonly occurs through the construction of cattle tanks, and such structures undoubtedly affect disturbance regimes of channel springs downstream; however, such effects have yet to be studied.

Ungulate Foraging: The foraging of large ungulates, such as cattle, horses, sheep, elk, deer, can devastate springs ecosystems by removing vegetation cover, altering plant and invertebrate assemblages, increasing erosion, and contaminating surface water (Grand Canyon Wildlands Council 2002). These impacts may be further intensified if the source is fenced to control ungulate movement.

Ungulate Trampling Impacts: Livestock grazing continues to exert pervasive adverse influences on springs and other riparian habitats because riparian zones provide water, shade, and succulent vegetation (Bauer and Burton 1990, Chaney et al. 1990, Fleischner 1994, Grand Canyon Wildlands Council 2002). Although livestock grazing impacts on springs have received relatively little attention, much attention has been devoted to understanding, assessing, and improving management of grazed wetland and riparian habitats (i.e., U.S. Department of the Interior 1993).

Exotic Plant and Animal Invasions: Widespread introduction of non-native species may similarly greatly compromise ecological functioning at springs. The susceptibility of springs ecosystems to invasion by alien (non-native) species is a complex function of interactions among abiotic and biotic factors, introduction history, and invading species autecology (Lonsdale 1999). Non-native species are abundant at springs across the southern Colorado Plateau (Grand Canyon Wildlands 2002). Stevens et al. (in prep) report that non-native species in northern Arizona and southern Utah include at least 247 plant, 7 invertebrate, 39 fish, 1 amphibian, 2 reptile, 8 bird, and 13 mammal species. Stevens and Ayers (2002) reported that alien plant and animal species were abundantly but unevenly distributed across seven groups of ecosystems in the Grand Canyon region. A total of 155 alien vascular plant species (10.4% of the total flora) and 33 alien vertebrates (7.3% of the total vertebrate fauna) were detected there. In contrast to Elton's (1958) prediction that invasibility should be negatively correlated with diversity, recent studies report spatial scale-dependent and fertility-related positive correlations among alien and native plant species diversity (Wiser et al. 1998, Lonsdale 1999, Stohlgren et al. 1999, 2003). The Colorado River corridor, other riparian areas including springs, and areas with high densities of roads and livestock trails had the highest densities of alien species. Alien species richness and density vary among ecosystems there in relation to relative productivity and relative disturbance intensity, and alien diversity was positively correlated with native biodiversity. Therefore, it appears that highly diverse ecosystems, such as springs, are most prone to alien invasions and attendant changes in composition, trophic structure, and function. These studies provide welcomed insight into habitat invasibility and alien population eruptions which are among the most significant, long-lasting and complex anthropogenic impacts on the world's ecosystems.

Although the life history strategies of eruptive alien species have been studied (e.g., Brotherson and Field 1987, Pysek et al. 1995, Holway 1999), many efforts to predict which introduced species will erupt and where eruptions compromise ecosystem integrity have met with limited success (e.g., Noble 1989, Pysek et al. 1995). In part this is because alien population eruption often occurs irregularly across spatial scales and among habitats and ecosystems within a biome (Horvitz et al. 1998). Also, alien eruption may be greatly delayed after initial colonization: Kowarik (1995) reported that on average 147 yr elapsed between introduction and eruption of alien populations around Brandenburg, Germany.

Fire Effects: The impacts of anthropogenic fire on springs have been little studied. Graham (in prep.) presents data on the slow recovery responses of a hanging garden to visitor-caused fire in southern Utah. The Grand Canyon Wildlands Council (2002) presented limited data indicating the potentially more rapid recovery of a spring than adjacent coniferous forest in northern Arizona. However, Graham (in prep.) reported that recovery of a burned hanging garden spring in southern Utah was remarkably slow. Evidence from the White Mountain Apache Tribe indicates that springs wetland vegetation at White and other springs may recover relatively quickly after forest fires, but that springs were collaterally damaged by increased sheet flow erosion and channel-cutting (Burnette et al. 2003). Research in progress in Hart Prairie by Springer indicates that reintroduction of fire to upland forests above wet meadows has the potential to increase water yield to the wet meadows.

Visitor Impacts: Recreational use impacts at springs have long been a concern at springs in some National Park Service units with management attention focused at Vaseys Paradise and other recreationally heavily used springs in Grand Canyon and at hanging gardens in Zion National Park. In most cases, creation and maintenance of discrete trails greatly reduces visitor impacts at springs; however, focused visitation is likely to affect larger wildlife populations and reduce springs-uplands trophic linkage.

Mining: The impacts of mines on springs may involve ground and surface water abstraction, diversion, regulation, or pollution, as well as construction and processing impacts and disturbances. Mine dewatering operations can significantly alter groundwater discharge to springs.

Traditional and Science-related Collecting Impacts: Trampling may occur during traditional uses and research. Such disturbances may or may not affect springs ecosystem processes depending on the size and type of the spring, its susceptibility to disturbance, and the intensity of activity. Overharvesting may be an issue in ethnobiology, and handling of rare fish or other vertebrate species may reduce population viability. For example, concern exists that tag-marking and electro-shocking of a great percentage of the total adult humpback chub may be implicated in the decline of this endangered fish species in Grand Canyon.

Management Action Impacts: Management actions to protect springs often simply involve site closure, prohibiting visitation, or creation of discrete trails to allow visitors to reach the springs but limit their impacts. If done without inventory and assessment information, such actions may actually damage, rather than help recover, the springs ecosystem. For example, fencing livestock out of a spring source may allow excess vegetation to develop eliminating surface water and threatening aquatic species persistence (Grand Canyon Wildlands Council 2002). Maintaining a sufficient disturbance regime to create some open water and space may be an important management decision. Creation of a surfaced trail to facilitate visitation (e.g., as occurs at some hanging garden springs) may eliminate leaf litter and prohibit movement of land snails and other invertebrate species. However, erosion can become a serious influence on springs geomorphic integrity if management fails to construct and maintain a trail to a regularly visited springs source. Restoration actions also may affect springs ecosystems, particularly if restoration goals fail to consider the range of natural variability of discharge, habitat area, and natural environmental impacts, such as fire, flooding, or rockfall.

Stressors Model Structure

Overview: We present a general state-and-transition model of human impacts on springs ecosystem characteristics and types (Figs. 2, 19). The natural springs ecosystem condition is regarded as the reference condition and is subject to natural variation in flow, geochemistry, aquifer responsiveness to climate variation, landscape disturbance (i.e., flooding, rockfall, native primary consumer herbivory), productivity, nutrient dynamics, population dynamics, and biogeographic processes as described in the controls model. The stressors model involves assessment of several physical pre-orifice, at-orifice, and post-orifice human impacts, as well as several biological at-orifice and post-orifice impacts. We first consider these impacts on springs characteristics overall and then consider the effects of selected stressors on the springs types identified by Springer et al. (in prep.; Table 2) as occurring on the Colorado Plateau. We then conduct a more refined analysis of four stressors (groundwater depletion, post-orifice diversion, severe livestock overgrazing, and severe infestation of non-native plant species for all springs types and microhabitat types (13 common microhabitats are associated with subaerial Colorado Plateau springs). Our analyses indicate that groundwater depletion is the largest and most universal threat to springs ecosystems, and we explore its influence on the overall controls model. Several may be the most useful indicators of anthropogenic stresses, including springs flow, water quality, microhabitat area, vegetation cover, and populations of sensitive species (i.e., endemic or listed species).

Stressor Impacts on the Controls Submodels

Overview: Numerous human impacts affect springs ecosystems. Stressor impacts on the controls submodels vary considerably by type, intensity, timing, and interaction factors (Fig. 19). Here we describe the basic impacts of the common stressors on submodel processes.

Climate-PhysicalGeological-Aquifer Dynamics Submodel 1 Stressors*:* Although elevation and geologic effects on springs are relatively static, the probability functions of climate variables shifts in response to global climate changes. The effects of climate changes may be partially predictable in space-for-time analyses of ecosystem distribution across elevation on the Colorado Plateau. Subtle shifts towards warmer temperatures and lower relative humidity may have large landscape impacts on, for example, the lower elevational distribution of ponderosa pine (*Pinus ponderosa*) and other economically important trees. Paleorefuge springs that are protected from groundwater pumping are likely to serve as islands of ecological constancy during global climate change, as soil moisture relations are less dependent on short-term climate changes.

The above physical and climate impacts affect groundwater quality or quantity through aquifer recharge dynamics. Such changes may be short-term (individual precipitation event), or long-term (response to climate change, or human activities). A diminution of the quantity of recharge may influence groundwater quality. As an aquifer naturally drains, older water may discharge from the aquifer. Typically the longer the residence time of water in an aquifer, the longer the water has to react with the minerals in the aquifer to increase the mass of dissolved solids. Water quality may also be changed by an increase in recharge to an aquifer. In aquifers that are highly fractured or faulted, precipitation and/or runoff may rapidly recharge the aquifer. Springs discharging from karst aquifers in limestone are typically flashy (i.e., discharge responds rapidly to precipitation and runoff).

Recharge from treated wastewater, irrigation return flow, or other activities which return water to aquifers may change the quality of water in the aquifer. Typically, humans load salts, nutrients, or organic pollutants to the water. Nitrogen and orthophosphate concentrations are naturally low in groundwater; however, anthropogenic agricultural pollution has greatly increased in springs systems in some portions of the United States, and nutrient augmentation may affect some Colorado Plateau springs. Turbidity of the water also may be elevated if it is influenced by rapid recharge from surface runoff.

Geomorphology Submodel 2 Stressors: Human alteration of groundwater quality may alter calcium carbonate precipitation or other processes that influence local geomorphology. The impacts of direct geomorphic changes on the orifice and first 100 m of runout stream are more conspicuous. Springs sources are commonly excavated, slotted piping is installed, and the spring is reburied to capture culinary flow. Also, springs boxes or houses may be constructed over source. Such practices are mandated by the U.S. Environmental Protection Agency and individual States which require that culinary springs water not be exposed to the surface. Such practices are geomorphically devastating to the springs ecosystem. Construction activities for livestock or wildlife watering is also common including excavation of the source and lining the runout stream to improve capture or transfer of flow.

Microclimate Submodel 3 Stressors: While human actions have limited impacts on geological site configuration variables, such as elevation and aspect, human impacts on global climate and aquifer discharge are large. Global climate change is resulting in warmer regional climate conditions that potentially reduce or eliminate discharge at springs. These factors are likely to increase microsite temperature and PET and alter flows and the ameliorating influences of springs water temperature on microhabitat distribution.

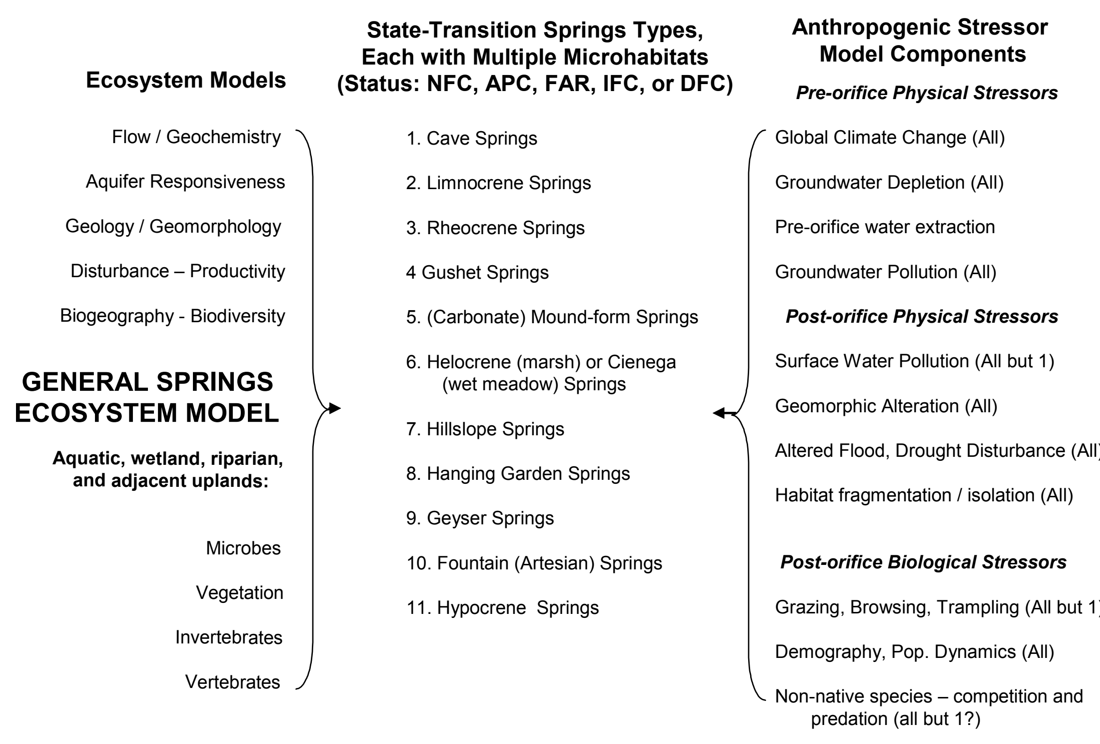


Fig. 19 : State-and-transition, and anthropogenic alteration mechanics springs ecosystem models. State transitions based on springs types from Springer et al. (in press). Ecological functioning: NFC – natural functioning condition; APC – affected functioning condition; FAR – ecologically functioning at risk, impaired; IFC – impaired functional condition; and DFC – dysfunctional functioning.

Disturbance-Productivity Regime Submodel 4 Stressors: Anthropogenic alteration of springs flow regimes takes place through groundwater extraction and surface water diversion, or alteration. In addition, global climate change is likely to alter storm and drought frequency with unknown effects on the magnitude and duration of resulting disturbances.

Return flow of agricultural or urban waters may augment shallow aquifer springs flows, in some cases creating springs or increasing flows. Construction of Glen Canyon Dam and Lake Powell have created numerous new springs along the downstream tailwaters, and these springs have been colonized by a wide array of native and non-native plant species, including maidenhair fern (*Adiantum capillus-veneris*) and helleborine orchid (*Epipactis gigantea*; L.E. Stevens, unpublished data).

Habitats Template Submodel 5 Stressors: Groundwater depletion, flow diversion, water pollution, and human habitat alterations are the primary stressors of springs microhabitats. Springs microhabitats may be reduced in area, lose function, or be lost entirely from any of these impacts. Loss or reduction of habitat area is generally a dosage-dependent impact; however, dewatering is likely to be a threshold response, rather than a gradual response. Most perennially wet habitats and associated aquatic fauna are extremely susceptible to the initial dewatering. Subsequent dewatering events are not likely to exert much further impact.

Biogeography Stressors: Human impacts to regional biogeography involve loss of species at all spatial scales and increasing habitat fragmentation and loss (decreasing colonization probability and increasing the likelihood of extirpation). In addition, the widespread introduction of non-native species may decrease springs ecosystem permeability and the colonizability of springs by native dispersing taxa.

Trophic System Stressors: Ecosystem dynamics are often disrupted by anthropogenic interference with species composition (particularly that of non-native species), alteration of population dynamics, and habitat structure. Introduced species also create novel trophic anomalies and disruptions.

Ecosystem Goods and Services Stressors: Sustained over-harvest of water, biological resources, and esthetic resources (i.e., visitation) characterizes the management of unprotected springs and is likely to severely degrade springs ecosystem integrity, limit sustainability, and result in ecological failure of the springs as an ecosystem.

Responses of Springs Characteristics to Common Stressors

Most anthropogenic stressors exert complex, interactive impacts on springs ecosystem characteristics. Based on our experience with nearly 300 springs on the southern Colorado Plateau, we estimated the responses of 15 common springs ecosystem characteristics to 14 common types of human stressors (Table 8). We assigned a qualitative negative, neutral, positive, or combination impact rating to each pairwise combination. This analysis revealed that 54 percent of the pairwise interactions between ecosystem characteristics and stressors were likely to be negative, only 3 percent were neutrao-positive, and 23.8 percent were considered uncertain. The following ranking of stressor negative impact strength applies across this array of ecosystem traits:

Groundwater depletion = Pre-orifice flow diversion = Agriculture =
Recreational visitation > Roading = Fuel harvesting = Ungulate trampling
> Ungulate grazing > Burning > Groundwater pollution > Non-native species introduction = Post-orifice diversion > Orifice construction >
Pre-orifice flow augmentation

However, if the numerous uncertain stressor effects shown in Table 8 are negative, the impacts of all stressors are strong and nearly equal except for post-emergence flow and pre-orifice flow augmentation which are only weakly negative.

Orthogonal analysis of the Table P data show which ecosystem traits are most strongly negatively affected by the full array of anthropogenic stressors:

Native plant cover = Native plant diversity = Microhabitat connectivity >
Native pop. sizes = Soil quality = Plant standing biomass >
Ecological efficiency = Microhabitat area = Microhabitat quality >
Water quantity > Nutrient availability > Productivity >
Non-native species dominance > Nutrient spiral length > Water quality

Table 8: Qualitative impacts of 14 common human stressors on 15 springs ecosystem characteristics. Signs indicate the direction of impact on the ecosystem characteristic. ± indicates that the impact may be in either negative or positive direction. Evaluations are based on LES and AES unpublished observations on >300 springs in northern Arizona.

Ecosystem Traits	GW depletion	GW pollution	Pre-emergence flow diversion	Pre-orifice flow augmentation	Post-emergence flow diversion	Orifice construction, fencing	Livestock or wildlife grazing	Livestock or wildlife trampling	Burning	Road construction	Fuel harvesting	Agriculture	Non-native species introductions	Recreational visitation	Neutral-positive	Potentially negative	Uncertain	Neg. + Uncertain
Ecological efficiency	-	±	-	0+	-	±	±	-	-	-	-	-	±	0-	1	9	4	13
Habitat area	-	±	-	0+	-	±	±	-	-	-	-	-	±	0-	1	9	4	13
Habitat connectivity	-	±	-	0+	-	-	-	-	-	-	-	-	±	0-	1	11	2	13
Habitat quality	-	-	-	0+	-	±	±	-	±	-	-	-	±	0-	1	9	4	13
Native Diversity	-	-	-	0+	-	±	-	-	±	-	-	-	-	0-	1	11	2	13
Native plant cover	-	±	-	0+	-	±	-	-	-	-	-	-	-	0-	1	11	2	13
Native pop. Sizes	-	-	-	0+	-	±	-	-	±	-	-	-	±	0-	1	10	3	13
Non-native dominance	±	±	±	0+	±	0+	±	±	±	+	+	+	+	0+	7	0	7	7
Nutrient availability	-	±	-	0+	-	±	±	±	±	-	-	-	±	0-	1	7	6	13
Nutrient spiral length	±	±	0+	0-	0+	0+	0+	0+	±	0+	+	±	±	0+	8	1	5	6
Productivity	-	±	-	0+	-	±	±	-	±	-	-	-	±	0-	1	8	5	13
Soil quality	-	±	-	0+	-	±	-	-	-	-	-	-	±	0-	1	10	3	13
Standing biomass	-	±	-	0+	-	±	-	-	-	-	-	-	±	0-	1	10	3	13
Water quality	0	-	0	0	0	0	-	-	0	0	0	0-	0	0-	9	5	0	5
Water quantity	-	0	-	+	0	0-	0	0	0+	0	0	0	0-	0	10	4	0	4
Neutral or positive	1	1	2	14	11	3	3	3	2	4	4	2	1	3				
Total negative	12	4	12	1	3	2	7	11	6	11	11	12	3	12				
Uncertain	2	10	1	0	1	10	6	2	7	0	0	1	11	0				

As above, if the numerous uncertain stressor effects shown in Table 8 are negative, the impacts of stressors strongly affects all ecosystem characteristics strongly and equally except non-native species dominance, nutrient spiral length, and water quantity and quality. The apparently odd exception of these latter two characteristics is attributable to the issue that of all the stressor variables considered, only groundwater depletion and pre-orifice diversion strongly negatively affect flow. Of course, these two variables are among the most important components of springs ecosystem integrity.

Collectively, these stressors result in species and microhabitat loss and fragmentation; however, the pathways through that process vary by stressor and springs type. Physical pre-orifice stressors like climate change and groundwater depletion may affect core ecosystem processes including aquifer dynamics, and springs flow and water quality. Such impacts may be difficult or impossible to reverse. Other pre-orifice impacts include: groundwater pollution, groundwater extraction from the immediate pre-orifice environment, and diversion of surface waters that may feed the orifice. Physical stressors operating on the orifice itself involve the common practice of sealing fissures to focus flow, orifice collapse due to manipulation, diversion of water in the orifice, orifice enclosure in springs boxes and houses, and access-related impacts. Post-orifice impacts include partial or total flow diversion, construction or development, fencing, road construction, surface water pollution. Sociobiological/management stressors on the post-orifice environment include non-native species invasions; direct or indirect loss of species; ungulate grazing, particularly by livestock; and recreational or visitor impacts. While some post-orifice alterations may be reversible, some geomorphic impacts (e.g., site development) and biological impacts (e.g., species losses) may be as devastating to ecosystem integrity as is dewatering through groundwater depletion.

Stressor-induced States-and-Transitions

We identified five state transitions for 19 common types of anthropogenic stressors that affect springs based on changes in ecosystem characteristics and as compared to the natural ecosystem condition (Table 9). These five transition states of ecosystem health were:

- If human impacts are not detectable, the springs may exist in the natural functioning condition (NFC = ecosystem health level 5)
- If human activities have minor but detectable impacts on ecosystem health and the natural condition is readily restored, the springs ecosystem is regarded as being in a slightly altered functioning condition (AFC = level 4).
- Springs that are functioning at risk (FAR = level 3) have obvious and threatening impairment of ecological function and integrity because human impacts on the aquifer, the landscape at and surrounding the orifice, or regional-global climate; however, restoration potential is likely to be high at these sites.
- Springs that are largely destroyed by human activities, but still retain some natural flow and native species, and have a questionable potential for restoration or rehabilitation are regarded as being in a jeopardized functional condition (JFC = level 2).
- Springs that have been entirely destroyed by direct or indirect human activities and exist in a fully degraded, dysfunctional condition (DFC = level 1).

The management regime must also be considered in concert with a springs ecosystem condition. Acceptable management results if an analysis of the springs ecosystem condition is in accord with the intent of the management program even if the springs ecosystem is fully diverted and ecologically obliterated. Of course, we recommend that managers not fully dewater any spring, but we recognize that springs managers often choose to manage a spring for a dysfunctional condition. In contrast, springs that are out of compliance with land use plans require and deserve management attention.

Table 9: Stressor impact scoring and criteria for springs under five levels of impairment: natural functional condition (NFC), altered functional condition (AFC), functioning at risk (FAR), jeopardized functional condition (JFC), and dysfunctional condition (DFS).

Human	Impacts by Ecosystem Functional State				
Impact	NFC	AFC	FAR	JFC	DFC
Physical Pre-orifice Impacts					
Climate change	Climate changes are within natural range of variability resulting in natural range of variation in aquifer dynamics, springs flow, springs, and species and associated microhabitat distributions	Climate is slightly altered resulting in a slight shift in the natural range of variation in aquifer dynamics, springs flow, and springs species and associated microhabitat distributions	Climate is significantly altered resulting in a dramatic reduction in the natural range of variation in aquifer dynamics, springs flow, and springs species and associated microhabitat distributions	Climate is greatly altered, or climate changes have been persistent resulting in a >80 % reduction in the natural range of variation in aquifer dynamics, springs flow, and springs species and associated microhabitat distributions	Microhabitats, species, and ecological function eliminated by major, persistent climate changes
Groundwater depletion	Microhabitats, vegetation cover, native fauna with natural variation; no water table declines or flow abstraction	Slightly reduced water table elevation, potential loss of springflow-wetted and riparian microhabitats, microhabitat area, and species	Substantially reduced water tables, flow; loss of springs microhabitat area, vegetation cover, fauna; dewatering eminent	Dewatering has occurred, substantial water table declines; little remaining springs flow or flow has become seasonal or erratic; little habitat, cover, or fauna remaining	Water table below level that supports any springs emergence; no remaining flow, virtually complete loss of springs microhabitats and native biodiversity
Groundwater pollution	Microhabitats, vegetation cover, native fauna with natural variation; no evidence of pollution or groundwater contamination impacts	Slight pollution impacts reduce or increase productivity, slight alteration of native species distribution, diversity	Substantially reduced or increased ecological function, long-term impairment of soils, reduced habitat area or fauna, or greatly increased vegetation cover	Vegetation, invertebrate, fiah, wildlife, and ecological severely integrity threatened by decreased water quality and accumulation of pollutants	Ecological function eliminated by pollutants
Extraction from the orifice	Flow, microhabitats, vegetation cover, native fauna with natural variation	Slightly reduced flow, minor loss of wetted and riparian microhabitats; some construction impacts	Substantially reduced flow and habitat area, vegetation, cover, fauna; obvious construction impacts	Little remaining flow; loss of most aquatic, wetland, and riparian species and ecological function; substantial construction impacts	No remaining flow, virtually complete loss of native biodiversity; major construction impacts
Loss of upstream waters	No re-routing of surface water away from infiltration zones; no impact on flow variability; microhabitats, vegetation cover, native fauna with natural variation	Some re-routing of surface water away from infiltration zones; slight impact on flow variability; microhabitats, vegetation cover, native fauna slightly affected	Extensive re-routing of surface water away from infiltration zones; reduced springs flow variability; microhabitats, vegetation cover, native fauna strongly affected	Little remaining nearby surface flow, or perennial flow has become seasonal or erratic; little habitat, cover, or fauna remain	Upstream flow eliminated by diversion of nearby surface flow; loss of microhabitats and native species.

Human Impact	Impacts by Ecosystem Functional State				
	NFC	**AFC**	**FAR**	**JFC**	**DFC**
Orifice impacts					
Sealing fissures	Flow, microhabitats, vegetation cover, native fauna with natural variation; no restriction on wall crack habitats or fauna	Slight reduction in wall seepage or flow; wall-sealing impacts apparent by minor	Substantial reduction in wall seepage or flow; wall-sealing reduces microhabitats and species distribution	Most wall seepage or flow eliminated; wall-sealing reduces species and microhabitat data	All wall seepage or flow eliminated; no crack microhabitat space remaining
Structural collapse	Flow and geomorphology consistent with natural springs type; springs ecological function natural	Flow and geomorphology slightly inconsistent with natural springs type; springs ecological function slightly altered	Flow and geomorphology strongly altered by geomorphic alteration of orifice area; inconsistent with natural springs type; springs ecological function strongly altered	Flows and ecological function almost completely altered by geomorphic disruption of orifice area	Geomorphic disruption of orifice area has devastated the springs as an ecosystem
Diversion	Flow, microhabitat areas, vegetation cover, native fauna, subject to natural variation	Minor but detectable reduction in microhabitat area, vegetation cover, native fauna, natural flow variation due to flow diversion at orifice	Loss of microhabitat area, vegetation cover, native fauna, and natural flow variation threatens ecosystem integrity	Most microhabitat area, vegetation cover, native fauna, and natural flow variation lost due to diversion at orifice	Ecological integrity lost through desiccation by diversion at orifice
Enclosure	Microhabitats, vegetation cover, native biota with natural variation; no noticeable orifice enclosure impacts	Microhabitats, vegetation cover, native biota with slightly restricted natural variation; slight but noticeable orifice enclosure efforts	Microhabitats, vegetation cover, native biota with strongly restricted natural variation; obvious, serious orifice enclosure efforts	Microhabitats, vegetation cover, native biota and ecosystem function virtually eliminated by spring box or spring house construction; construction impacts threaten ecological function	Microhabitats, vegetation cover, native biota and ecosystem function eliminated by construction of springs box or house; construction impacts overwhelming
Access impacts	No trails or other access impacts visible	Trails, ladders, ropes, access-related erosion impacts on orifice and ecosystem are slight	Trails, ladders, ropes, access-related erosion impacts on orifice and ecosystem substantia lresulting in site erosion and obvious species and microhabitat impacts	Trails, ladders, ropes, access-related erosion impacts on ecosystem are extensive resulting in ecosystem-threatening site erosion and microhabitat loss and impairment	Ecosystem loss through trailing and associated access-related erosion

Human Impact	Impacts by Ecosystem Functional State				
	NFC	**AFC**	**FAR**	**JFC**	**DFC**
Post-orifice Physical Impacts					
Partial or total flow diversion	Microhabitats, vegetation cover, native biota with natural variation; no noticeable flow alteration	Microhabitats, vegetation cover, native biota with slightly reduced natural variation; limited but detectable flow alteration	Ecological integrity of microhabitats, vegetation cover, native biota threatened by flow alteration	Microhabitats, vegetation cover, native biota mostly eliminated by flow alteration; little remaining ecological integrity	Microhabitats, vegetation cover, native biota irretrievalby eliminated by flow alteration; no remaining ecological integrity or restoration potential
Construction, development (spring houses, stock yards, stock tanks, etc)	Microhabitats, vegetation cover, native biota with natural variation; no noticeable site manipulation	Microhabitats, vegetation cover, native biota with nearly natural variation; slight but noticeable site manipulation	Microhabitats, vegetation cover, native fauna with moderate levels of natural variation; site development impacts conspicuous and ecologically disruptive	Microhabitats, vegetation cover, native fauna, and ecological integrity nearly obliterated by heavy levels of construction impacts; limited restoration potential	Microhabitats, vegetation cover, native fauna, and ecological integrity eliminated by construction impacts; no potential for recovery
Fencing	Microhabitats and vegetation cover, native biota movement unimpeded by fences	Microhabitats and vegetation cover, native biota movement slightly affected by fences	Microhabitats, and vegetation cover, native biota movement strongly affected by fences	Microhabitats and vegetation cover, native biota movement virtually completely restricted or exclosed by fences	Microhabitats and vegetation cover, native biota movement eliminated by fencing
Road construction	Microhabitat and vegetation cover, native biota unimpeded by road presence or use	Microhabitat and vegetation cover, native biota movement slightly impeded by road presence or use; slight, but noticeable road impacts	Microhabitat and vegetation cover, native biota movement strongly impeded by road presence or use; obvious road impacts	Microhabitat and vegetation cover, native biota movement virtually eliminated by road presence or use; ecosystem function highly threatened by road impacts	Microhabitat and vegetation cover, native biota movement prevented by road presence and use; overwhelming road impacts and little restoration potential
Surface water pollution	Microhabitats, vegetation cover, native fauna with natural variation and reproductive potential; little evidence of pollution impacts	Slight pollution effects reduce or increase productivity, alter native species distribution, diversity; may be cumulative and lead to DFC	Substantially reduced ecological function, long-term impairment of soils, reduced habitat area, vegetation cover, fauna due to surface pollution	Vegetation, invertebrate, fiah, wildlife, and ecological integrity threatened by decreased water quality and accumulation of pollutants	Ecological function eliminated by surface water pollution
Post-orifice Biological Impacts					
Native species loss	Natural assemblages in appropriate densities are present and self-sustaining	Slight but detectable reduction in natural diversity, slightly impaired self-sustainability and ecosystem function	Strong alteration of natural diversity and impairment of self-sustainability and ecosystem function	Natural diversity, self-sustainability, and ecosystem function nearly lost, but some species and processes appear to be recoverable.	Natural diversity, self-sustainability, and ecosystem function destroyed, no potential for recovery.

Human Impact	Impacts by Ecosystem Functional State				
	NFC	**AFC**	**FAR**	**JFC**	**DFC**
Post-orifice Biological Impacts Continued					
Non-native species invasion	Non-native species impacts undectable on natural habitat distribution, native species population dynamics, and ecosystem function.	Minor ecosystem impacts of non-native species on natural habitat distribution, native species population dynamics, and ecosystem function.	Conspicuous ecosystem impacts of non-native species, including natural habitat alteration, alteration of native species population dynamics and nutrient dynamics.	Overwhelming ecosystem impacts of non-native species, with most natural microhabitats disrupted, native populations and ecosystem function highly threatened.	Unrecoverable ecosystem impacts of non-native species on habitat distribution and structure, population dynamics, and ecosystem function
Ungulate use	Microhabitats, vegetation cover, native fauna with natural variation and reproductive potential; little evidence of ungulate use (grazing, browsing, trampling, wastes)	Minor evidence of ungulate grazing, browsing, trampling, or waste; microhabitats, vegetation cover, native fauna with slightly compromised natural variation and reproductive potential.	Conspicuous evidence of ungulate grazing, browsing, trampling, or waste; microhabitats, vegetation cover, native fauna with substantially compromised natural variation and reproductive potential.	Ungulate grazing, browsing, trampling, or wastes seriously threaten microhabitats, vegetation cover, and native fauna natural variation and reproductive potential.	Unrecoverable ecosystem impacts of ungulate impacts.
Recreation	Microhabitats, vegetation cover, native fauna with natural variation and reproductive potential; little evidence of recreation impacts	Microhabitats, vegetation cover, native fauna variation and reproductive potential slightly compromised by recreation impacts (recreation, trailing, waste, etc.)	Microhabitats, vegetation cover, native fauna populations substantially compromised by recreation impacts (visitors, trailing, waste, etc.)	Microhabitats, vegetation cover, native fauna populations with little remaining integrity because of recreation impacts (visitors, trailing, waste, etc.)	Unrecoverable ecosystem impacts due to recreation

A Preliminary Examination of Model Predictions

We estimated and scored the relative ecological integrity of 11 springs types and ≤13 associated microhabitats in relation to the dysfunctional condition (DFC) of each of four common anthropogenic stressors: aquifer depletion and springs dewatering, post-orifice depletion, and severe ungulate grazing or non-native species infestation. We scored each pairwise spring type by microhabitat cell on a 1-5 scale (Fig. 20). Cells were left blank in cases where microhabitats were not likely to be associated with a springs type (e.g., hypocrene springs are unlikely to support spray zone microhabitats). Thus, low scores in this analysis represent low ecosystem integrity, whereas high scores represent near-natural conditions.

This analysis indicated strong differences between severe stresses from four sources on springs ecosystem integrity. The following order of severity of anthropogenic impacts was observed:

Groundwater depletion >> Post-flow diversion >
Severe livestock grazing > Severe infestation of non-native species

The above pattern was consistent for all springs types except cave springs (which were only strongly affected by groundwater depletion) and hypocrene springs (where no post-orifice diversion occurs). The similarity of response of most springs types to the array of stressors was surprising, with only geysers having relatively higher scores than other surface-flowing springs.

Groundwater Depletion A

	Springs Habitats													
Spring Type	Cave Interior	Orifice	Hyporheic	Wet Wall	Madicolous	Spray Zone	Open-water pool	Spring Stream	Low-slope Wetlands	Hillslope Wet Meadow	Riparian	Adjacent Dry Rock	Adjacent Uplands Linkage	Springs Microhabitat Diversity Index
Cave	2	1	1	1	1	1	1	1				3	1	1.30
Limnocrene	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Rheocrene	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Gushet	2	1	1	1	1	1	1	1	1	1	1	2	1	1.15
Mound-form	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Helocrene	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Hillslope	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Hanging garden	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Geyser	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Fountain	1	1	1	1	1	1	1	1	1	1	1	2	1	1.08
Hypocrene	1		1						1	1	1	2	1	1.14
Mean Microhabitat Occurrence	1.18	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	2.09	1.00	1.11

Post-orifice Diversion B

	Springs Habitats													
Spring Type	Cave Interior	Orifice	Hyporheic	Wet Wall	Madicolous	Spray Zone	Open-water pool	Spring Stream	Low-slope Wetlands	Hillslope Wet Meadow	Riparian	Adjacent Dry Rock	Adjacent Uplands Linkage	Springs Microhabitat Diversity Index
Cave	5	1	2	5	3	1	5	5				5	5	3.70
Limnocrene	1	2	2	1	1	1	1	1	1	1	2	2	3	1.46
Rheocrene	3	5	2	1	1	1	1	1	1	1	2	4	3	2.00
Gushet	4	5	1	1	1	1	1	1	1	1	2	4	3	2.00
Mound-form	1	5	1	1	1	1	1	1	1	1	2	4	3	1.77
Helocrene	1	2	2	1	1	1	1	1	1	1	2	2	2	1.38
Hillslope	1	2	2	1	1	1	1	1	1	1	2	2	2	1.38
Hanging garden	1	3	2	3	2	2	1	1	1	2	2	3	3	2.00
Geyser	1	5	1	2	2	2	1	1	1	1	2	4	2	1.92
Fountain	1	5	1	2	2	2	1	1	1	1	2	3	2	1.85
Hypocrene	1		1						3	4	4	5	5	3.29
Mean Microhabitat Occurrence	1.82	3.50	1.55	1.80	1.50	1.30	1.40	1.40	1.20	1.40	2.20	3.45	3.00	2.07

Ungulate Grazing C

	Springs Habitats													
Spring Type	Cave Interior	Orifice	Hyporheic	Wet Wall	Madicolous	Spray Zone	Open-water pool	Spring Stream	Low-slope Wetlands	Hillslope Wet Meadow	Riparian	Adjacent Dry Rock	Adjacent Uplands Linkage	Springs Microhabitat Diversity Index
Cave	5	1	2	5	3	1	5	5				5	3	3.50
Limnocrene	1	2	2	1	1	1	2	3	1	1	2	3	3	1.77
Rheocrene	3	4	2	2	2	2	2	3	1	1	2	3	3	2.31
Gushet	4	4	2	2	2	2	2	3	1	1	2	3	3	2.38
Mound-form	1	3	2	2	2	1	2	3	1	1	2	3	3	2.00
Helocrene	1	2	2	2	2	1	2	2	1	1	2	2	3	1.77
Hillslope	1	2	2	2	2	1	2	2	1	1	2	2	3	1.77
Hanging garden	1	3	2	3	2	2	3	3	1	2	2	3	3	2.31
Geyser	1	4	2	2	2	2	3	3	1	1	2	3	2	2.15
Fountain	1	4	2	2	2	2	3	2	1	1	2	3	2	2.08
Hypocrene	1		1						1	1	2	3	3	1.71
Mean Microhabitat Occurrence	1.82	2.90	1.91	2.30	2.00	1.50	2.60	2.90	1.00	1.10	2.00	3.00	2.82	2.16

Non-native Species Infestation D

	Springs Habitats													
Spring Type	Cave Interior	Orifice	Hyporheic	Wet Wall	Madicolous	Spray Zone	Open-water pool	Spring Stream	Low-slope Wetlands	Hillslope Wet Meadow	Riparian	Adjacent Dry Rock	Adjacent Uplands Linkage	Springs Microhabitat Diversity Index
Cave	5	1	2	5	3	1	5	5				5	5	3.70
Limnocrene	1	4	2	1	1	1	4	3	2	1	3	2	3	2.15
Rheocrene	3	4	2	2	3	2	2	3	2	1	3	4	3	2.62
Gushet	4	4	3	2	3	2	3	4	2	2	3	4	4	3.08
Mound-form	1	4	1	2	3	1	2	3	2	1	2	4	2	2.15
Helocrene	1	2	2	2	2	1	2	2	3	2	3	2	4	2.15
Hillslope	1	2	2	2	2	1	2	2	3	3	3	2	4	2.23
Hanging garden	1	2	2	3	3	3	3	3	2	3	3	3	4	2.69
Geyser	1	5	2	2	3	2	3	3	2	1	2	4	3	2.54
Fountain	1	5	2	2	3	2	3	2	2	1	2	3	3	2.38
Hypocrene	1		1						2	2	2	3	4	2.14
Mean Microhabitat Occurrence	1.82	3.30	1.91	2.30	2.60	1.60	2.90	3.00	2.20	1.70	2.60	3.27	3.55	2.53

Fig. 20: Spring type – habitat matrix with DFC for human impacts of: (A) groundwater depletion and pre-orifice diversion; (B) post- orifice diversion; (C) severe livestock overgrazing; and (D) severe infestation of non-native vegetation. Numbers represent ecological function of the microhabitat with coupled natural and anthropogenic stressors: 1 – low ecological functionality to 5 – high functionality (missing values for habitats not naturally occurring).

Orthogonal analysis of the above data revealed that microhabitat types responded variably to the four severe stresses across all springs types (Fig. 21). In order of impact severity, the same pattern was observed as in the springs microhabitat diversity analysis (above) with the impacts of groundwater depletion strongly outweighing the other stressors, but all four having profound impacts on springs ecological health. Exceptions to this general pattern included higher impacts of grazing on orifices, low-gradient wet meadows, hill-slope wet meadows, and riparian habitats, as compared to post-orifice diversion.

In addition, above-ground stressor impacts on springs microhabitats appear to increase in severity with distance from the orifice (Fig. 22). Non-native vegetation, overgrazing, and post-orifice diversion impacts generally were modest near the orifice, and became more severe in microhabitats more distant from the orifice. The exception to this pattern was groundwater depletion, which severely affects all microhabitats except adjacent dry rock surface habitats.

This is a preliminary analysis, and refined understanding is needed with empirical data compilation and quantitative modeling to better understand trends and thresholds of ecosystem integrity in response to stressors. Single stressor impacts may affect many, if not all, of the controls submodels, and we have attempted to depict how the single factor of groundwater depletion affects the full array of submodels (Fig. 23). Not only does groundwater depletion affect aquifer dynamics and water quality, but also disturbance intensity, cave and aquatic and riparian habitats, species presence and distribution, and feedback of ecosystem goods and services to the habitat template. Unfortunately, few anthropogenic stressors occur or act independently in space and time, and interactive effects may further exacerbate stressor impacts on springs ecosystems. Nonetheless, this analysis provides preliminary insight into the responses of spring and their microhabitats to these and other human stressors.

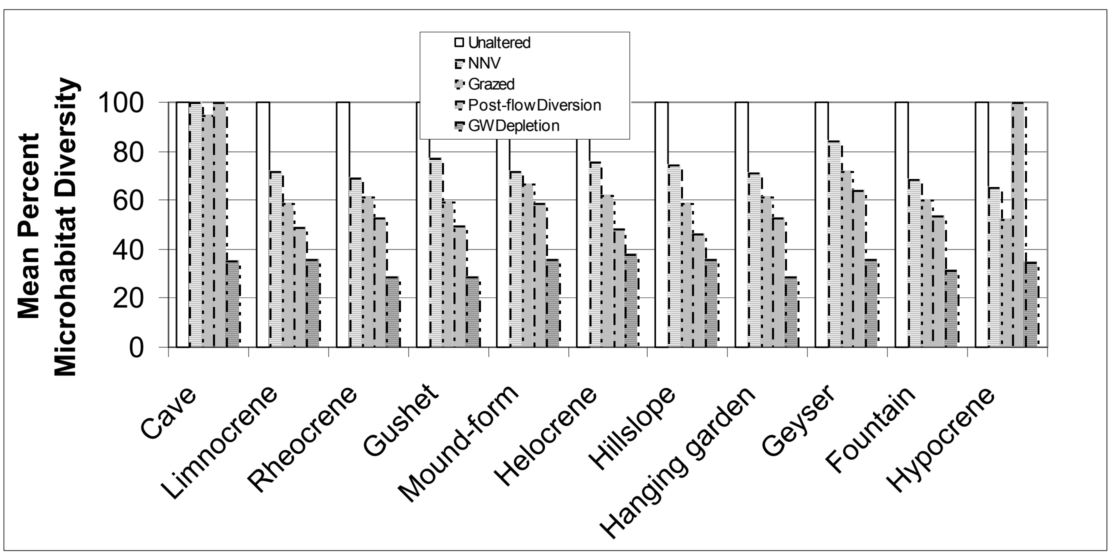


Fig. 21: Predicted relative impacts of severe anthropogenic stress (DFC) on the mean relative microhabitat diversity of 11 springs types on the Colorado Plateau. Stressors include: Grazed – severely overgrazed by ungulate herbivores; GW Depletion – springs desiccation through groundwater depletion; NNV – high levels of non-native vegetation; post-flow diversion of springs flow; unaltered, natural condition.

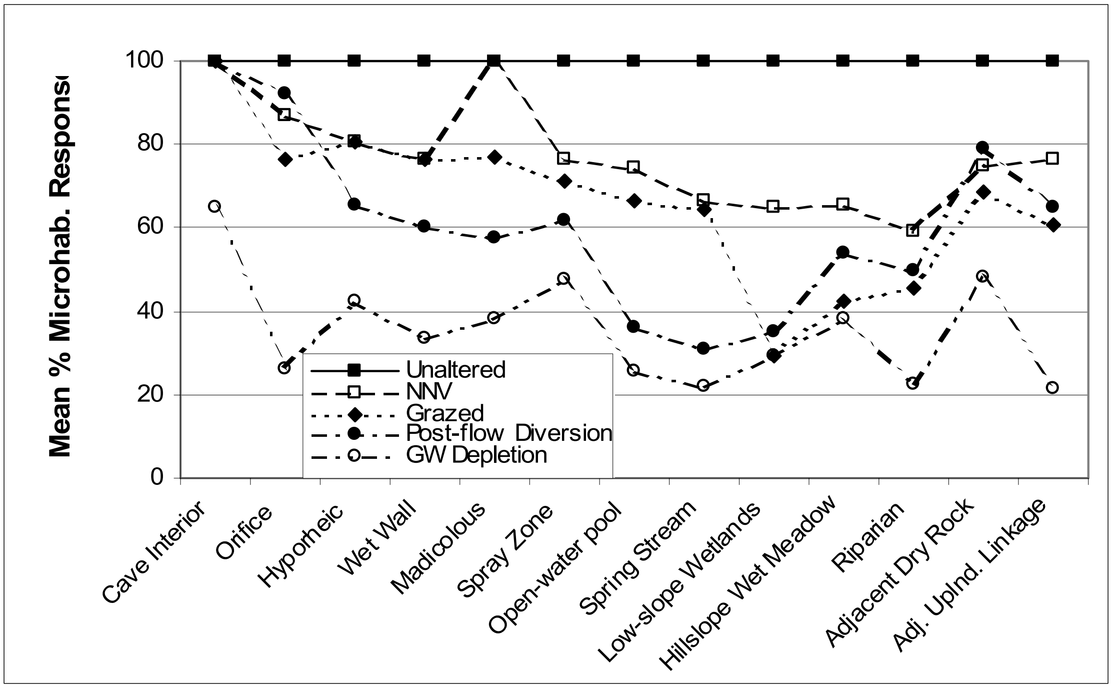


Fig.22: Predicted relative impacts of four DFC anthropogenic stressors on the ecological integrity of 13 springs microhabitats types on the Colorado Plateau. Stressors include: Grazed – severely overgrazed by mammalian herbivores: GW Depletion – springs desiccation through groundwater depletion; NNV – high levels of non-native vegetation; post-flow diversion of springs flow; unaltered, natural condition.

Utility of the Stressors Model: Early Warnings

The general springs state-transition model (Fig. 19) is influenced by a wide array of interacting human impacts operating at a range of spatial and temporal scales including groundwater depletion; habitat fragmentation/isolation; flow regulation (including dewatering); groundwater and/or surface water pollution; livestock grazing, browsing, and trampling; altered flood and drought disturbance intensity; population demography and dynamics shifts; non-native species introductions; and global climate change. Analysis of such influences requires abundant empirical, spatially explicit classificatory, inventory, and mapping data, which do not presently exist for most landscapes or springs ecosystems. Once such data are acquired for a large landscape, these state-transition models should assist management by guiding selection of indicators, monitoring protocols, and sampling designs; contributing to the development of early warning indications; and helping prioritize springs ecosystem management in relation other altered ecosystems within a landscape.

The anthropogenic stressors model describes how key anthropogenic stressors disrupt natural interactive controls and alter springs ecosystem structure and function. From a monitoring perspective, this model component provides warning of likely state transitions; however, three factors make early warning of flow reduction problematic: 1) aquifer water table elevation controls over springs flow operate at fine scales and are poorly known; 2) water table declines are often rapid and are difficult to monitor; and 3) the initial dewatering of a perennial springs may be biologically disastrous. As a consequence, warnings may come too late for appropriate management action. In cases of post-emergence habitat alteration and not otherwise involving flow, adequate early warning may be obtained for appropriate management decisions. Here we describe and illustrate how groundwater depletion, livestock grazing, and alien plant invasion disrupt interactive controls and alter ecosystem structure/function.

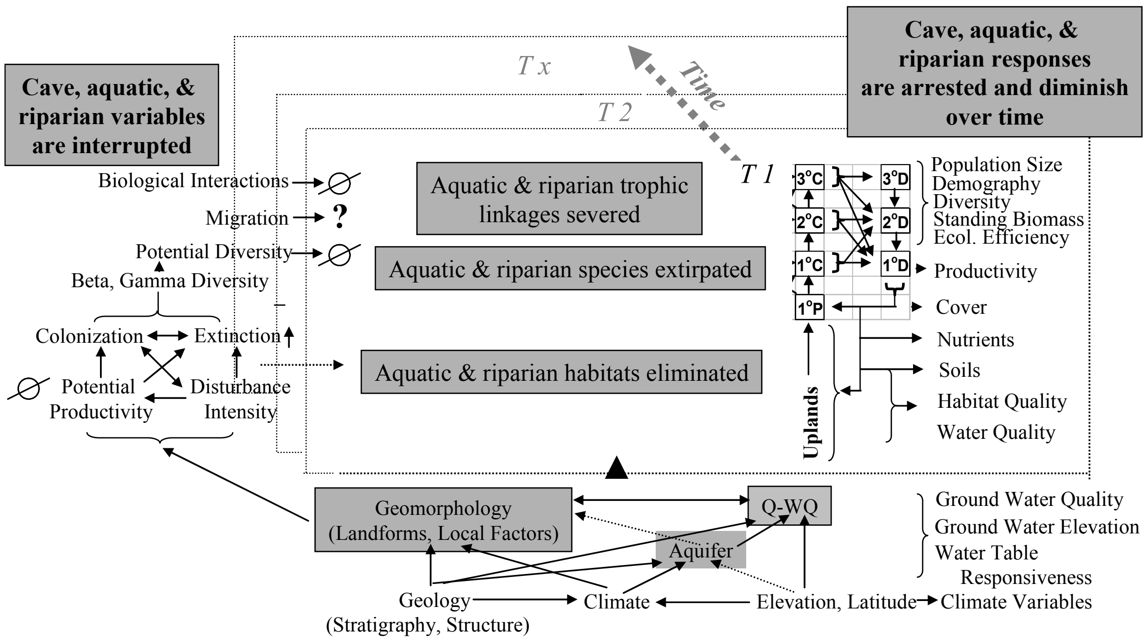


Fig. 23: Impacts of groundwater depletion or pre-emergence diversion on the springs ecosystems controls model. °C – consumer, °D – decomposer, °P – pirmary producer; T1-x is time one to time x.

Recommendations

Deriving predictive outputs from this springs conceptual model will be a challenge because so few of the actual variable relationships are presently empirically understood. However, the conservation of springs is of great importance and urgency. This urgency may encourage managing agencies to adopt a crisis mode of management; however, the essential issues of inventory, assessment and prioritized restoration remain to be conducted. The development of a springs ecosystem model proposed here is a long-term science matter, but if the issues discussed in this document are built into the inventory, assessment, research, and monitoring process, some of these submodels may be refined in the near future. Information gathered on springs will considerably add to the presently limited information base, and all such information is needed to improve long-term conservation of these remarkable ecosystems.

A trophic approach eventually may become useful for shifting from this conceptual framework towards quantitative prediction by emphasizing the common metric of ecosystem energy derived from, and stored, through organic production. Ecosystem energetics analysis was first described by Lindeman (1942) in Cedar Bog Lake and Lake Mendota. Subsequently, Odum (1957) related ecosystem energetics to the processes of succession and refined those metrics at Silver Springs, Florida. Odum's study related ecosystem energetics to trophic structure. When coupled with landscape modeling of habitat patch dynamics, this approach should serve to integrate springs ecosystem processes and components, by quantifying interactions between state variables, physical processes, and natural and anthropogenic stressors in relation to springs response variables (e.g., vegetation cover, biodiversity, population variables) that are most likely to be important for monitoring, management and springs restoration. Although too few springs have been analyzed to provide general conclusions about patterns of trophic efficiency at different kinds of springs, this approach may be fruitful for predictive modeling in the future.

Out in the real world, springs are disappearing at an alarming rate, and most of that loss goes largely unrecognized (Stevens and Meretsky in prep.). National and international initiatives are needed to bring attention to the ecological importance of springs and their conservation. We recommend that springs managers consider promptly implementing inventory and assessment protocols, as well as emergency response measures to cope with immediate threats to their springs ecosystems. Much additional basic information is needed, and new administrative and technical approaches are needed for long-term protection and restoration of springs ecosystems. In addition, it would be appropriate to select a suite of springs for intensive research purposes, so that fundamental and outstanding questions on natural springs ecosystem ecology can be addressed.

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Appendix A:

Description of Log Pearson Type III Analysis
(Texas Department of Transportation 2004)

Graphical demonstration of disturbance frequency may best be assessed using the Log-Pearson Type III analysis. This is a statistical distribution method that has gained the most widespread acceptance and is recommended by the Texas Department of Transportation (2004) and many other flood frequency analysts. It is a statistical analysis of gauged flood data or other continuous and variable data. The analysis for natural flows involves the following steps:

1. Acquire and assess the annual peak discharge record. The record should comprise only one discharge (maximum) per year.
2. Calculate the logarithm of each discharge value.
3. Use Equation 1, Equation 2, and Equation 3 to calculate the following statistics:

Equation 1: $$\overline{Q}_L = \frac{\sum X}{N}$$

Equation 2: $$S_L = \left\{ \frac{\sum X^2 - \frac{\left(\sum X\right)^2}{N}}{N-1} \right\}^{\frac{1}{2}}$$

Equation 3: $$G_S = \frac{N^2\left(\sum X^3\right) - 3N\left(\sum X\right)\left(\sum X^2\right) + 2\left(\sum X\right)^3}{N(N-1)(N-2)S_L^3}$$

In these equations, N is the number of observations, X is the logarithm of the annual peak discharge, SL is the standard deviation of the logarithms of the annual peak discharge, and GS is the coefficient of skew of log values (station skew).

4. Use Equation 4 to calculate the logarithm of the discharge for each frequency

$\overline{Q}$

Equation 4 : $\log Q = \quad_{L} + KS_{L}$

where QL is the mean of the logarithms of the annual peak discharges, Q is the flood magnitude, K is a frequency factor for a particular return period and coefficient of skew (values of K for different coefficients of skew, G, for specified return periods).

5. Plot discharge versus frequency on standard log probability paper.

6. Consider adjusting the calculations to accommodate a weighted skew and accommodating outliers in the data.